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Inhomogeneity of visual space, discontinuity of perceptual time and cultural imprinting as exemplified with experiments on visual attention, aesthetic appreciation and temporal processing

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Zusammenfassung

Eines der wichtigsten Argumente für einen kognitivistischen Zugang zur Psychologie ist, dass sich die Psychologie nicht grundlegend von der Physik zu unterscheiden scheint; mentale Phänomene sind offenbar unmittelbar auf physikalische Realität bezogen. Beginnend mit der Psychophysik seit dem neunzehnten Jahrhunderts haben Experimente gezeigt, dass dieser Denkansatz nicht nur mit großen Vorteilen, sondern auch mit einigen Fallstricken verbunden sein kann. Auf der Basis des zugrundeliegenden Konzepts, dass mentale Phänomene physikalischen Ereignissen unmittelbar zugeordnet werden können, wird automatisch angenommen, dass die zeitliche Verarbeitung von sensorischen Informationen kontinuierlich sei, wie es das Zeitkonzept in der klassischen Physik nahelegt. Dieses Konzept widerspricht der Möglichkeit einer diskreten zeitlichen Informationsverarbeitung, wie sie in der Tat gilt. Des weiteren wird davon ausgegangen, dass Informationsverarbeitung in einem homogenen visuellen Wahrnehmungsraum eingebettet ist; dies ist jedoch nicht der Fall. Es wird dargestellt, dass mit einfachen sensorischen Reizen oder komplexen ästhetischen Stimuli und deren experimenteller Manipulation ein brauchbares empirisches Paradigma für ein besseres Verständnis von kognitiven Mechanismen bereitsteht, das auf diskrete zeitliche Verarbeitung und einen inhomogenen visuellen Wahrnehmungsraum hinweist. In mehreren Experimenten wird gezeigt, daß die Modulation der Aufmerksamkeit im Gesichtsfeld nicht homogen ist; Reaktionszeitexperimente mit spezifischen Modifikationen stützen die Hypothese, dass

funktionell zwei Aufmerksamkeitssysteme im Gesichtsfeld eingebettet sind. Weitere unterstützende Beobachtungen über die Inhomogenität des Gesichtsfeldes kommen aus Experimenten zur ästhetischen Wahrnehmung westlicher und östlicher Kunstwerke. Diese Forschung bestätigt überdies das allgemeine Konzept von anthropologischen Universalien sowie kulturellen oder individuellen Spezifika bei der ästhetischen Wahrnehmung. Im Hinblick auf die zeitliche Wahrnehmung weisen Histogramme der Reaktionszeit auf diskrete zeitliche Informationsverarbeitung hin, was sich auch aus Beobachtungen der zeitlichen Ordnungsschwelle herleiten läßt. Bei der Untersuchung verzögerter Reaktionen wird gezeigt, dass eine präzise zeitliche Kontrolle erst nach einem längeren Intervall erreicht wird. Zusammenfassend kann man aus den verschiedenen Experimenten herleiten, dass mentale Prozesse im räumlichen und zeitlichen Bereich zwar offenkundig nicht direkt zugänglich sind, doch sollte dies nicht als eine undurchdringliche Barriere angesehen werden, um Mechanismen mentaler Prozesse zu entschlüsseln. Mit den klar definierten physikalischen Stimuli und der genauen Beachtung von Stationaritätsbedingungen bei Messungen kann diskrete zeitliche Verarbeitung und Inhomogenität des visuellen Wahrnehmungsraums gezeigt werden.

Abstract

One of the most compelling arguments for a cognitivist approach to psychology is that psychology does not seem to be fundamentally different from physics; mental phenomena appear to be directly related to physical reality. Experimental evidence beginning in the nineteenth century with psychophysics has shown that this approach can offer great benefits, but can suffer from some pitfalls as well. On the basis of the underlying concept that mental phenomena match directly physical events, it is automatically assumed that temporal processing of sensory information is continuous as it is assumed in classical physics neglecting the possibility of discrete temporal information processing, which in fact is the case. Furthermore, it is assumed that information processing is embedded in a homogeneous perceptual visual space; this is not the case. It is shown that the use of simple sensory stimuli or complex aesthetic stimuli and their experimental manipulation provide a useful empirical paradigm for a better understanding of the cognitive mechanisms, i.e., indicating discrete temporal processing and an inhomogeneous perceptual visual space. A number of experiments show that attentional modulation is not homogeneous in the visual field; observations using the reaction time paradigm with specific modifications support the hypothesis that two attention systems are functionally embedded in the visual field. Further supportive findings about the inhomogeneity of the visual field come from experiments on the aesthetic perception of Western and Eastern artworks. This research also confirms in addition the general concept of anthropological universals

and cultural or individual specifics in aesthetic appreciation. With regard to temporal perception, reaction time distributions suggest discrete time sampling which can also be derived from observations on temporal order threshold. When testing delayed reactions after stimulus presentation, it is shown that precise temporal control is reached only after a rather long interval. It can be concluded on the basis of the different experiments that even though mental processes in the space and time domain are obviously not directly accessible, this should not be considered as an impenetrable barrier to unravel the mechanism of mental processes. Employing well-defined physical stimuli and strictly observing stationarity conditions in measurements indicate discreteness in temporal processing and inhomogeneity of visual space.

Introduction

We are creatures living in space and time. Our technologies change the ways in which we perceive space and time, but cannot eliminate the fact that we live in space and time. The properties of space and time are profoundly different for physical and psychological processes, respectively. Physical time and space are ordinal, monotonic, and usually homogeneous. Psychological time and space exhibit paradoxical, disorderly, and inhomogeneous properties in a wide variety of phenomena that seem to conflict with those of physical time and space (Uttal, 2008).

According to the philosopher Henri Bergson (1889/2001), there are two kinds of time, homogeneous and heterogeneous. The latter is the time of our experience, and is named by him as 'la durée'. Homogeneous time, which is what we ordinarily mean when we use the word time, is, in his view, space, on to which the mind merely projects psychological time, the succession of our conscious states, thus making it appear to be a successive and continuous reality. In fact, it is nothing but an illusion for there is no true succession in things which are said to be measured by time, since one state has entirely disappeared when another appears. So he wrote: "Doubtless exterior things change, but their moments only succeed one another with respect to a consciousness which remembers them. We observe outside us, at any given moment, a collection of simultaneous positions; nothing remains of the former simultaneities".

This concept of a moment has important consequences for an understanding of psychological processes. The time point with a finite duration can also be looked at as a "temporal window" within which events are constructed, which are the building blocks for our conscious activity (Pöppel, 1994, 1997, 2009). Evidence suggests that the brain may house distinct temporal windows functioning at different duration ranges, for instance distinct psychophysical characteristics at different timescales (Ulbrich, Churan, Fink, & Wittmann. 2007), performance being selectively impaired for different temporal ranges under a dual-task paradigm (Miyake, Onishi, & Pöppel, 2004), or different brain regions being activated for sub- and supra-second intervals (Koch, Oliveri, & Caltagirone, 2009; Wiener, Turkeltaub, & Coslett, 2010). The existence of inhomogeneous timing mechanisms likely contributes to our ability to cope with a constantly changing environment, and understanding their cognitive processes and neural bases is, thus, a key goal of behavioral psychology and neuroscience.

The inhomogeneity in cognitive processes is not only time dependent, but also depends on space. In the analysis of the experience of space, psychologists study perceptions to obtain meaning or understanding of the concept of space (Birx, 2009). Psychological space is created out of mental activity. In this respect, space is that which allows us to differentiate multiple identical and simultaneous perceptions from one another. When we fixate a location in a scene, visual inhomogeneity prevents the perceived image from having equal resolution throughout. Thus, we see the outside world through a window of varying resolution such that fine detail is available only within a small area around the fixation point (García-Pérez, 1989). The radius of this area covers approximately the central 2° of visual angle (Lavidor & Walsh, 2004). Visual inhomogeneity is a well-known and well-established property of early visual processing.

Further evidence supporting the inhomogeneity of visual representation is indicated in oculomotor or attentional control when different response modes are observed as function of stimulus eccentricity. More specifically, using the experimental paradigm of "inhibition of return" (IOR) an eccentricity effect of attentional control in the visual field has been shown indicating an inhomogeneity of visual processing, i.e., the magnitude of IOR is much stronger at the periphery (e.g., 21°) relative to the perifoveal (e.g., 7°) visual field (Bao & Pöppel, 2007; Bao, Wang, & Pöppel, 2012), showing different processing mechanisms for perifoveal compared to more peripheral stimuli. This eccentricity effect of IOR is independent of the cortical magnification factor (Bao, Lei, Fang, Tong, Schill, Pöppel, & Strasburger, 2013), and resistant to subjects' practice (Bao, Sander, Trahms, Pöppel, Lei, & Zhou, 2011). It has been proven to be a robust phenomenon which is substantiated also by observations using imaging technologies, i.e., fMRI (Lei, Bao, Wang, & Gutyrchik, 2012), and MEG (Zhou, Bao, Sander, Trahms, & Pöppel, 2010). This confirms previous observations like the inhomogeneity of sensitivity throughout the visual field (Pöppel & Harvey, 1973; Strasburger, Rentschler, & Jüttner, 2011). However, paradoxically, one observes constancy of brightness of supra-threshold stimuli throughout the visual field, which suggests homogeneity of the visual field on the subjective level (Zihl, Lissy, & Pöppel, 1980). We suggest that this paradox can be overcome if one uses the basic concept of the reafference principle in which sensory and motor aspects of behavior are integrated (von Holst & Mittelstaedt, 1950). Subjective visual phenomena can lead to unexpected but testable hypotheses of neural processing on the structural and functional level in the early visual pathway (Zhou et al., 2016; publication No. 1).

Given the aforementioned observations suggesting different modes for processing stimuli in the perifovea compared to the periphery of the visual field, we conducted experiments trying to further investigate whether attentional control also operates inhomogeneously between our most effective system for achieving high-resolution visual perception, i.e., foveal processing, and the relatively lower-resolution perifoveal vision (1° vs. 7°). The results displayed a similar eccentricity profile of an exogenous attention effect between foveal and perifoveal regions, which supports the concept that attention control is inhomogeneous in the visual field, with larger modulation effects of exogenous cues for perifoveal than foveal targets (Yang, Zhang, & Bao, 2015; publication No.2).

An increasing body of evidence supports the notion that explicit perceptual processing requires participation of attentional mechanisms. For instance, spatial covert attention can improve contrast sensitivity, spatial resolution, and processing speed for stimuli at the attended location (for a review, see Carrasco, 2011). However, since these effects have mainly been observed during task periods in which stimuli did not change, they cannot be extrapolated to change-detection tasks. More importantly, the inhomogeneity of attentional control in the visual field has been unexplored and not discussed in most of these studies. Therefore, the aim of our study is to investigate the effect of exogenous and endogenous attention on speed change detection thresholds in perifoveal and near-peripheral regions (5° vs. 10°), thereby assessing the generality of the inhomogeneity of attentional modulation in the visual field. The results suggest that exogenous attentional modulation is dissociable between the perifoveal and near-peripheral regions of the visual field, whereas endogenous modulation has an equal effect at the two eccentricities tested (Yang, Strasburger & Bao, 2018; publication No. 3).

The inhibitory component of attention - IOR has been found in both detection and discrimination tasks with later onset in discrimination tasks probably due to a higher processing demand. We examined whether the processing demand of cues can also modulate IOR in a detection task. The task to the peripheral cues, either color or gap cues, was passive viewing in one session (single task) and discrimination in another session (dual task). The results showed that the time course of IOR was resistant to the cue processing, while the magnitude of IOR was increased when the processing load became larger in dual task relative to single task. These results indicate that IOR in target detection is both reflexive in that its temporal dynamics remains invariant, and flexible in that its magnitude is modulated by task requirement (Zhou, Yang, & Bao, 2018; publication No. 4).

We keep thinking about the fact behind what we measure indirectly, and we come to call it attention. "Everyone", William James famously wrote, "knows what attention is" (James, 1890/1950). However, it is worth reflecting on what most people think they know about attention. Closer at hand, one of the pioneers of modern research on attention, Donald Broadbent emphasized the uncritical use of "attention" (Broadbent, 1982). A basic belief is that attention cannot be fully understood if isolated from the function it serves. Instead of talking about attention per se, a number of phenomena in attention research should be addressed in a more functional way, such as selectivity of perception, voluntary control over this selectivity, capacity limit, and interaction with higher cognitive processing. Thus, a further study was conducted showing that the role of attention is involved in the emotions perceived for example in music. We found evidence for an amplification of perceived emotions in the solitary listening condition, i.e. happy music was rated as happier and more arousing when nobody else was around and, in an analogous manner, sad music was perceived as sadder. This could be explained by the functions of attention: when listening to the music alone, increased attention allows us to enter more deeply into the idiosyncratic world and to explore emotions and feelings, thus happy music get even happier and sad music get even sadder (Zhang, Yang, Li, Pöppel, Bao, & Silveira, 2017; publication No. 5).

The music experiment reported here was designed to mimic the particular circumstance and the social situation in which the music is heard, i.e. listening to music alone or in the company of others. We believe that this ecological approach of using real world stimuli and scenarios allows a better insight into cognitive mechanisms. Especially, perceptual stimuli extracted from the arts like music, paintings or poetry allow a unique access to higher cognition complementing other experimental paradigms (Pöppel et al., 2013; Pöppel & Bao, 2017). We report here studies about different representations of the visual world in Eastern and Western art, which can further support the concept of visual inhomogeneity in the visual field. When traditional artworks between West and East are compared, Western and Eastern artists tend to use different perspectives to represent the visual world. Since the Renaissance, Western landscape paintings are rather precise reproductions of a visual surrounding (Kubovy, 1986), whereas Chinese painting are supposed to convey the experience of "being in nature" rather than “seeing nature”, which led to an arrangement of spatial information in a vertical manner with multi-layers on top of each other in a scroll form (Cameron, 1993; Sullivan, 1984; Law, 2011; Tyler & Chen, 2011). Our results showed that both Western and Chinese participants gave higher aesthetic ratings to traditional paintings from their own compared to the other culture. Besides, landscapes were more preferable than people in a scene across different cultural groups (Bao et.al, 2016; publication No. 6). In a following experiment of viewing Western and Chinese landscape paintings in an fMRI (functional magnetic resonance imaging) scanner, we observed an intracultural bias in the aesthetic appreciation of Western and Eastern traditional landscape paintings in European and Chinese participants. Europeans showed greater activation in visual and sensory-motor brain areas, regions in the posterior cingulate cortex, and hippocampus when viewing Western compared to Eastern landscape paintings. Chinese participants exhibited greater neural activity in the medial and inferior occipital cortex and regions of the superior parietal lobule in response to Eastern compared to Western landscape paintings (Yang et al., 2019; publication No. 7). We suggest these findings are possibly related to different perceptual habits and social practice in everyday life of different cultures.

It is worth noting that substantial evidence has already been gained about constraints on aesthetic appreciations from visual processing at the operational level. Aesthetic appreciations of a painting may have their source in extracting basic elements of stimuli already in the early visual pathway (Chatterjee & Vartanian, 2014; Cinzia & Vittorio, 2009; Zhou et al., 2016). In a recent study, we are looking for neural correlates of aesthetic appreciations in the work of the Chinese artist LaoZhu who represents the "third abstraction". The behavioral results show that original red paintings were preferred over its color-altered counterparts; the fMRI findings demonstrate that in comparison with the original red condition the color-changing paintings led to higher levels of activation in several brain regions, predominately in frontal and parietal cortex. It was likely due to the increased top-down control on the visual processing of color-altered paintings. We suggest that the aesthetic judgment is modulated as a function of low-level visual properties, and depends on the interplay of perceptual and higher order processes (Bao et al., 2017; publication No. 8).

Cultural specificity and its influence on cognitive processing can also be observed in timing tasks (Bao et.al, 2013). By comparing the temporal order thresholds (TOTs) between Chinese subjects with and without a secondary non-tonal language (i.e., English) experience, our study provides evidence supporting the concept that language experience can influence the auditory perception of temporal order. While Chinese subjects without English proficiency were good at discriminating the temporal order of two close frequency tones, Chinese subjects with English proficiency were good at both the close frequency and distant frequency order discrimination. Presumably Chinese as a tonal language imprints the brain in a selective way to develop a higher sensitivity for perceiving the temporal order of near frequency tones (Bao et al., 2013). At the same time, the difference between tonal language speakers with and without a secondary non-tonal language experience supports the neuronal plasticity for perceiving the order of frequency-related auditory stimuli. This study also indicates that the choice of an experimental paradigm can be essential for the conclusions to be derived (Bao et al., 2014; publication No.9).

Today, reaction time differences as an experimental paradigm to look into the complexity and dynamics of cognitive processing are widely employed in most psychological studies. This experimental paradigm goes back to the Dutch scientist Karl Donders (1868), who used simple and choice reaction times for a better understanding of mental operations. In this method of chronometric analyses, continuous temporal processing is usually assumed implicitly. However, there is a question: is time in the brain represented indeed as a continuous function? We provide evidence showing that multimodal reaction time distributions are often masked by experimental setups violating the stationarity conditions in measurements. The different patterns of reaction times described indicate that temporal processing on this level must be of discrete nature. We suggest that qualitatively different temporal mechanism are necessary to provide an operative basis for cognitive processing (Bao, Yang, Lin, & Pöppel, 2016; publication No. 10).

Discrete temporal processing can also be observed in other temporal domains. If a subject does not have to react as fast as possible to a stimulus, but has to delay the response by a predefined interval, this approach bears ecological meaning, because temporal information is used both for fast reactions and voluntary delayed actions, and the quantication of the passage of time is crucial for motor control. According to our observation, for shorter delayed responses the variance is very high, but for longer delayed responses the variance is significantly smaller although this phenomenon may appear contra-intuitive. Besides, there was a clear learning effect, i.e. the second half of trials showed much smaller response variety for all pre-defined delay times (Bao, Pöppel, Liang, & Yang, 2014; manuscript No. 11).

Finally, we emphasize that time windows that express discrete timing mechanisms in behavioral control and on the level of conscious experiences are the necessary bases to create cognitive order. The brain provides the temporal platform necessary for perception or attentional modulation, and being desynchronized, whatever the period of the investigated rhythm, can jeopardize brain function and associated health outcomes (Bao et al., 2015; publication No. 12).

Psychological space and time do not follow the same laws as their physical equivalents. The experiments and theoretical concepts described above indicate that perceptual space and experiential time are characterized by "discreteness" on the level of underlying mechanisms. Classical psychophysical studies or brain imaging experiments using simple or complex aesthetic stimuli support this notion in spite of the common sense impression of homogeneity of space and continuity of time. A true psychological science must attend to the aspects of behavior that are anchored to the physical world and eschew excursions into unsupportable theories and hypotheses concerning the nature of cognitive processes.

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Seeing without knowing: Operational principles along the early visual pathway

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Abstract: Single cases may lead to unexpected hypotheses in psychology. We retrospectively analyzed single case studies that suggested organizational principles along the early visual pathway, which have remained unanswered until now. First case: In spite of the inhomogeneity of sensitivity, paradoxically the visual field on the subjective level appears to be homogeneous; constancy of brightness of suprathreshold stimuli throughout the visual field is claimed to be responsible for homogeneity; specific summation properties of retinal ganglion cells are hypothesized to guarantee this effect. Second case: With a brain-injured patient having suffered a partial visual field loss it can be shown that color induction is a retinal phenomenon; lateral inhibitory processes at the level of amacrine cells are hypothesized as neural network. Third case: In a patient having suffered a bilateral occipital lobe infarction, some functional recovery has been demonstrated; divergence and convergence of projection in the ascending neural pathway are suggested as a structural basis for recovery. Slowed down binocular rivalry discloses a sequential mechanism in the construction of a visual percept. Fourth case: The pre-wired projection of the retina to the visual cortex in spite of a severe squint of one eye is confirmed, but paradoxically some local neuroplasticity is also suggested. Fifth case: Using habituation of local sensitivity in the visual field and its resetting by interhemispheric interactions as an experimental paradigm, it is suggested that spatial attention is controlled at the midbrain level. Sixth case: Observations on residual vision or “blindsight” support the hypothesis that the visual cortex is the one and only structure responsible for visual perception on a conscious level. The unifying principle of these retrospective analyses is that subjective visual phenomena can lead to unexpected but testable hypotheses of neural processing on the structural and functional level in the early visual pathway.

Keywords: attentional control; binocular rivalry; blindsight; brightness perception; color perception; consciousness; eccentricity effect; habituation; neuroplasticity; restitution of function

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Single case studies have shaped psychology and brain science since its very beginning in the 19th century. Such studies provide the unique opportunity to answer previously unasked questions (Pöppel et al., 2013), and to discuss what is usually taken as self-evident in subjective experiences. Single case observations may lead to unexpected hypotheses that have previously remained silent. Distinct lesions of the brain or observations with healthy subjects under unique circumstances can disentangle complex functions, for instance, according to the principle of "double dissociation of function" (Milner & Teuber, 1968), and they open new windows to understanding underlying mechanisms of cognitive processing (Martin & Hull, 2007). Cases like "Tan-Tan" (Broca, 1865), Henry M. (Scoville & Milner, 1957), and split-brain patients (Sperry, 1961) have opened new fields in the understanding of language, memory, visual perception, and other cognitive functions.

On the basis of a taxonomy of functions derived from evolutionary principles and neuropsychological observations (Bao & Pöppel, 2012; Pöppel, 1989; Zaytseva, Chan, Pöppel, & Heinz, 2015), it has been proven to be useful to distinguish between "content functions," which refer to the "what" of experiences like perceptions, memories, or emotions, and "logistical functions" or operational principles, like temporal control (Bao, Szymaszek, et al., 2013; Wang, Lin, Zhou, Pöppel, & Bao, 2015; Zhou, Pöppel, & Bao, 2014), attentional mechanisms (Bao & Pöppel, 2007; Singer, Zihl, & Pöppel, 1977), or activation of functions (Steriade, 1996), as modulated, for instance, by circadian rhythms (Aschoff, 1965; Bao et al., 2015; Zihl, Pöppel, & von Cramon, 1977). Operational principles provide the necessary basis for content functions; without logistical functions, as exemplified for instance by their disruption during anesthesia, mental content or "consciousness" would not be possible (Schwender, Madler, Klasing, Peter, & Pöppel, 1994), and disturbances on this logistical level result in impairments of cognitive processing (von Steinbüchel & Pöppel, 1993). In the retrospective analyses of single case studies from our own research environment, we disclose some operational principles for the early visual pathway from the retina to the visual cortex focusing on structural aspects of visual perception and on functional mechanisms on the neural level. These operational principles are implicit or "pre-semantic" (Pöppel & Bao, 2011); that is, they do not enter the level of conscious experiences, but they provide the necessary bases for visual perception. Importantly, specific predictions can be made from the phenomenal "high level" of visual experiences to the "low level" of their neural implementation.

Constancy of brightness throughout the visual field

In detailed measurements of increment threshold throughout the visual field to determine a two-dimensional sensitivity map (Pöppel & Harvey, 1973), one subject (E.P.) observed that the apparent brightness of threshold stimuli varied systematically throughout the visual field. Threshold targets at different eccentricities did not have the same apparent brightness (as was expected), but they appeared brighter in the periphery of the visual field. This observation was rather counterintuitive (and still is), as one would expect that at threshold for any location in the visual field the apparent brightness should be the same. Based on this initial observation, apparent brightness for suprathreshold targets was studied systematically both under photopic and scotopic adaptation conditions (Zihl, Lissy, & Pöppel, 1980). The results indicated that the apparent brightness of suprathreshold stimuli corresponded to their physical intensity, however, only for photopic adaptation conditions. This observation implies that the "operative range" between threshold brightness and supra-threshold brightness is getting continuously smaller for more peripheral visual targets (Figure 1).

Brightness constancy throughout the visual field can be considered as the functional basis for its homogeneity on the phenomenal level. Where in the afferent stream of visual information processing might brightness constancy, and as a consequence, homogeneity of the visual field, be created? For ecological reasons, one can assume that this process should be localized as early as possible, that is, already in the retina. If targets with equal physical brightness were to appear darker in the periphery of the visual field, as one would predict if apparent brightness were determined by multiples of threshold values (using traditional psychophysical reasoning), their chances of being detected would be worse compared to targets closer to the fovea. Using a teleonomic argument, it is, however, in the interest of optimal attentional control that, independent of where something will appear in the visual field, it should have equal probability of being detected. Only then could spatial attention be drawn without bias to any position in the visual field, and information appearing in the periphery of the visual field would not be neglected; only then could saccadic eye movements be programmed appropriately. As saccadic eye movements are elicited by stimuli that are projected to the superior colliculus in the midbrain, the compensatory mechanism to allow equal probability should be prior to the collicular processing stage. Thus, the creation of constancy of brightness should be implemented already in the retina. In this case, equal probability of responses towards

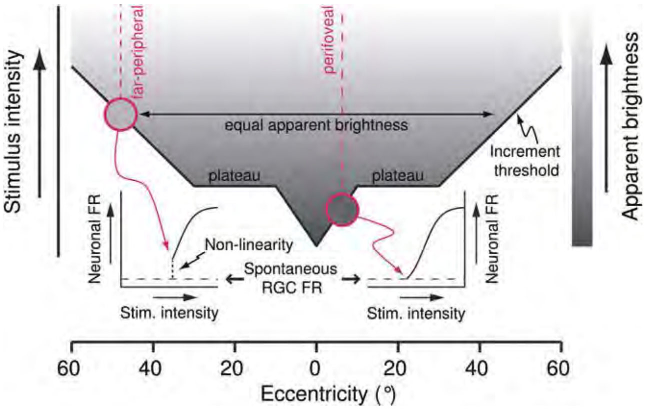

Figure 1. Distribution of increment threshold and apparent brightness along the horizontal meridian of the visual field under photopic adaptation and binocular viewing conditions. For more peripheral targets (red circle on the left) a higher stimulus intensity is required to reach increment threshold compared to perifoveal targets (red circle on the lower right). Measurements of apparent brightness show constancy of brightness throughout the visual field as indicated by the horizontal line. This phenomenon results in the effect that apparent brightness at threshold is higher for more peripheral targets as indicated by the vertical bar on the right side. For an explanation of different brightness levels for threshold stimuli on the neural level it is hypothesized that retinal ganglion cells show different summation properties for more peripheral compared to more central locations in the visual field. With increasing stimulus intensity, more central retinal ganglion cells (RGC) show a sigmoid summation curve (right lower insert) above the level of the spontaneous firing rate (FR), while more peripheral retinal ganglion cells show a non-linearity of summation at threshold (left lower insert) bringing the firing rate instantaneously to a higher level. (Figure abstracted from Zihl et al., 1980, and Roenneberg & Pöppel, 1985.)

unexpected visual stimuli anywhere in the visual field would be guaranteed.

How could this paradoxical situation be overcome already at the retina, that is, compensating for the decrease of sensitivity towards the periphery by creating contours of equal brightness throughout the visual field? The hypothesis is forwarded that more peripheral ganglion cells in the retina and their surrounding network are characterized by different summation properties compared to near-fovea ganglion cells (Figure 1, inserts); instead of a (more) sigmoid gain function in perifoveal regions, ganglion cells in the periphery should show a non-linearity of summation at threshold; the firing rate of retinal ganglion cells “jumps” from the level of the spontaneous firing frequency “instantaneously,” that is, with very short latency, to a higher level of firing frequency. This compensatory mechanism with different summation properties would explain why the apparent brightness is higher for peripheral targets. To the best of our knowledge, summation properties of ganglion cells in the primate retina, including the far periphery of the visual field, have not yet been investigated, although promising results have been obtained from the cat retina (Roenneberg & Pöppel, 1985). It should be noted that for the plateau region extending approximately between 10° and 35° eccentricity along the horizontal meridian, and from 10° to 20° eccentricity along the vertical meridian (Pöppel & Harvey, 1973), the same gain functions would be expected.

If the phenomenon of constancy of brightness is already implemented at the retinal level, another problem would also be solved in a bottom-up way, that is, that the apparent brightness is the same for the two halves of the visual field, even though they are represented in different hemispheres. In that case, no intercallosal interactions between the different hemispheric representations would be necessary with respect to equalizing brightness as they are getting the same information anyway. Furthermore, a top-down mechanism could be spared, that is, the apparent homogeneity of the visual field is thought to directly match the physical parameters of optical stimuli because common sense indicates that the “visual world” (Gibson, 1950) does not show any inhomogeneity with respect to lightness under photopic conditions.

Constancy of brightness throughout the visual field seems, on the surface, inconsistent with the dissociation of some attentional responses across eccentricities (Bao & Pöppel, 2007), such as the inhibition of return (IOR; Klein, 2000), which reflects the tendency of preventing attention from returning to previously cued locations. It has been shown that the IOR magnitude is significantly larger for peripheral (e.g. 21°) than perifoveal (e.g. 7°) locations, thus suggesting that spatial attention to perifoveal and peripheral visual targets is controlled by different mechanisms (Bao & Pöppel, 2007). This eccentricity effect is resistant to practice as is indicated by the relatively stable IOR difference between perifoveal and peripheral stimuli across experimental sessions (Bao et al., 2011), and it cannot be explained by the magnification factor (Bao, Lei, et al., 2013). It has been proven to be a genuine phenomenon that is substantiated also by observations using imaging technologies, for example, functional magnetic resonance imaging (fMRI; Lei, Bao, Wang, & Gutyrchik, 2012) and magnetoencephalogram (Zhou, Bao, Sander, Trahms, & Pöppel, 2010; Zhou, Sander, Trahms, Pöppel, & Bao, 2012). However, the dissociation of IOR does not contradict the constancy of brightness; it instead reflects that the attentional control in the perifoveal and peripheral regions differently involves the cortical and sub-cortical pathways (Bao & Pöppel, 2007); more importantly, it suggests that distinct mechanisms (at the cortical and sub-cortical level) are operating in the perifoveal and peripheral visual fields, consistent with the summation process of ganglion cells described above (at the retinal level). Although being controlled by different neural mechanisms, the perifoveal and peripheral IORs share the same time window (Bao, Wang, et al., 2013; Bao et al., 2015); they both approach the baseline at approximately 3 s after the onset of the visual cue. Such a common temporal control window, together with constancy of brightness, guarantees a unified spatiotemporal platform for visual processing.

Color induction at the retinal level

It has long been known that color vision is based on the selective stimulation of wavelength-sensitive receptors in the retina, and it has been shown that a cortical area is responsible for the colors we see on a subjective level (Wild, Butler, Carden, & Kulikowski, 1985; Zeki, 1980). The retinex theory of color vision (Land, 1983; Land, Hubel, Livingstone, Perry, & Burns, 1983) combines both retinal and cortical mechanisms, and it provides a theory of color constancy; one aspect of this integrative theory is that visual information has to be integrated over extended regions of the visual field to allow the construction of color constancy, that is, the color of an object is computed based on the ratios of radiation from the object and its surroundings that change little under different illuminations; the long-range color interactions are thus believed to be critical and the cortex is argued to be necessary for the achievement of color constancy. Taking this theory as a conceptual basis, the question arises as to how color induction (Brandt, Reiser, & Pöppel, 1988; Pöppel, 1986) might relate to the neural mechanisms attributed to the retinal and cortical structures. An experiment has been described (Pöppel, 1986), and is re-analyzed here, that suggests that color induction is most likely a retinal phenomenon, although functional mechanisms and detailed structural aspects have remained open until now. The conclusion that one deals in color induction with a retinal phenomenon has been made possible by the unique spatial configuration of a partial visual field loss in patient F.S., who had suffered a traumatic brain injury affecting the optic radiation (Stoerig, Kleinschmidt, & Frahm, 1998). The injury had resulted in the denervation of the left V1 and consequently an area of blindness in the right visual field (Figure 2, black area in the lower two panels); areas in the lower and upper part of the right visual field had remained functional.

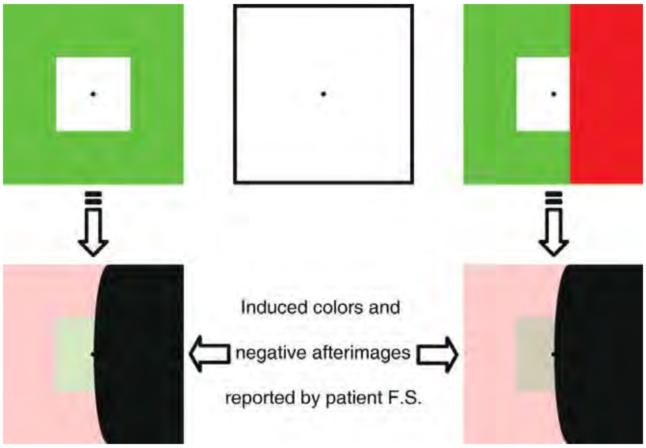

Figure 2. Experimental procedure to test color induction with a patient who has suffered a central injury resulting in an area of blindness in the right visual field (black area in the lower two panels). For details see text. (Figure abstracted from Pöppel, 1986.)

The experiment with the patient can be simulated by the interested reader: When fixating on the black dot in the center of the upper left panel of Figure 2 for some 10 s, a negative afterimage (magenta) for the green area and an induced color (green) for the white area is created; the afterimage and the induced color can be seen for some seconds when fixating on the black dot in the central white panel. When fixating on the central black dot in the upper right panel with the red area on the right for some 10 s, the hue of the central induced color is shifted towards grey when fixating on the black dot in the central white panel. The same difference of an induced color was reported by patient F.S. when the red area in the upper right panel was presented within the blind area indicated in black. The difference of the induced colors and the shift towards grey is simulated in the lower two panels. The patient reported the same differences of induced colors as the subjects with functional visual fields; however, he could not see the red area in the upper right panel. As has been demonstrated (Stoerig et al., 1998), this area of the visual field has no direct representation in the visual cortex. Thus, it can be concluded that color induction has to be neurally implemented prior to the visual cortex.

On the basis of this observation, it is suggested that a network already in the retina is possibly responsible for this effect. One has to look for a network with lateral interactions as color induction goes beyond local effects, and the most likely candidate would be the retinal layer of amacrine cells, which are known to have inhibitory interactions that are extended laterally, thus, covering large areas of the visual field (Chen, Hsueh, & Werblin, 2011). How might a neural machinery work, resulting in color induction? Here we represent a hypothesis, which, to the best of our knowledge, has not been tested: During an adaptation phase with different spectral components of light, local receptors within defined wavebands will fatigue. This results in a reduced lateral activity within the waveband-specific channels. Thus, in lateral areas to the adapted region, this specific component in white light will be disinhibited; this disinhibition results in an overemphasis of the adapted component when fixating on the white surface. As indicated, this neural hypothesis implies that the level of amacrine cells is characterized by an inhibitory lateral network that is waveband-specific.

Such an inhibitory network would guarantee functional stability with respect to color vision within the visual field, as not only local but extended regions in the visual field would be suppressed in the nonadapted phase when processing a local color stimulus giving this stimulus higher saliency. This lateral mechanism operates in a complementary way to local color processing. For a given position in visual space represented at one point on the retina, the different spectral channels are also inhibitory, as is demonstrated by negative afterimages. Thus, it is the complementarity of spatially distributed within-channel and localized between-channel inhibitions that is the basis for efficient color processing. If color constancy is created at the cortical level, as is implied by the retinex theory (Land, 1983), a lateral network necessary for color constancy might already be implemented in the retina. Indeed, although the color experience needs the involvement of cortical structures, the generation of long-range color interactions, as is demonstrated by the color induction (Pöppel, 1986), does not necessarily recruit cortical mechanisms argued by the retinex theory (Land, 1983; Land et al., 1983). It has to be noted that there is a functional relationship to constancy of brightness throughout the visual field as discussed above. As color constancy is a phenomenon based on neural processes extended throughout the visual field, constancy of brightness (Figure 1) is a functional prerequisite. Thus, the two mechanisms would have to be interconnected.

Restitution of visual function after a brain injury

Restitution of function after a brain injury has remained a challenging topic in neuropsychology. Several studies have shown that after systematic training, the functional visual field can be extended (Zihl, 1980; Zihl & von Cramon, 1985). The first patient in whom such extension could be demonstrated was probably patient H.H. (Pöppel, Brinkmann, von Cramon, & Singer, 1978), who had suffered a bilateral occipital lobe infarction sparing the neural representation of the foveal and perifoveal region of the visual field (Figure 3, right panel). What could be the functional and structural basis of such an improvement? The enlargement of the visual field removing blindness at the border of the scotoma is hypothesized to be structurally based on divergence of projection from the lateral geniculate nucleus (LGN) to the visual cortex (V1, Figure 3, upper left panel), and convergence of projection of projecting axons from the LGN to V1 (Figure 3, lower left panel). Both of these structural features (i.e., divergence and convergence) have been documented experimentally (Blasdel & Lund, 1983; Peters, Payne, & Budd, 1994). Thus, we hypothesize that after a cortical injury (as indicated by the dark ellipses), some visual information coming from the LGN, which has lost its primary projection field at V1, still has some cortical representation in adjacent neurons. With systematic training, synaptic efficacy of the remaining contacts is suggested to improve, resulting in functional recovery, although within limits.

This structural hypothesis raises several questions: What is the amount of divergence of projection from the retina to the LGN and from there to V1? How far does one have to "travel" laterally across the visual cortex until one is no longer getting a direct input from a defined retinal area? This question has to be turned around, as divergence of projection is necessarily complemented by convergence of projection: How much visual space (and retinal area) is represented within one local cortical position like a column in V1? There is both neuroanatomical and neurophysiological evidence indicating substantial divergence of projection (Gilbert & Wiesel, 1985) and a distributed representation in the visual system (Mitzdorf, Li, & Pöppel, 1994). Divergence of projection can also be indirectly deduced from the observation that after an occipital injury, the visual field loss is smaller for the temporal visual field compared to the nasal visual field (Engler, Zihl, & Pöppel, 1993); it has been argued that divergence of projection from the nasal retina representing the temporal visual field is larger because of the higher number of retinal fibers coming from the nasal retina compared to the temporal retina.

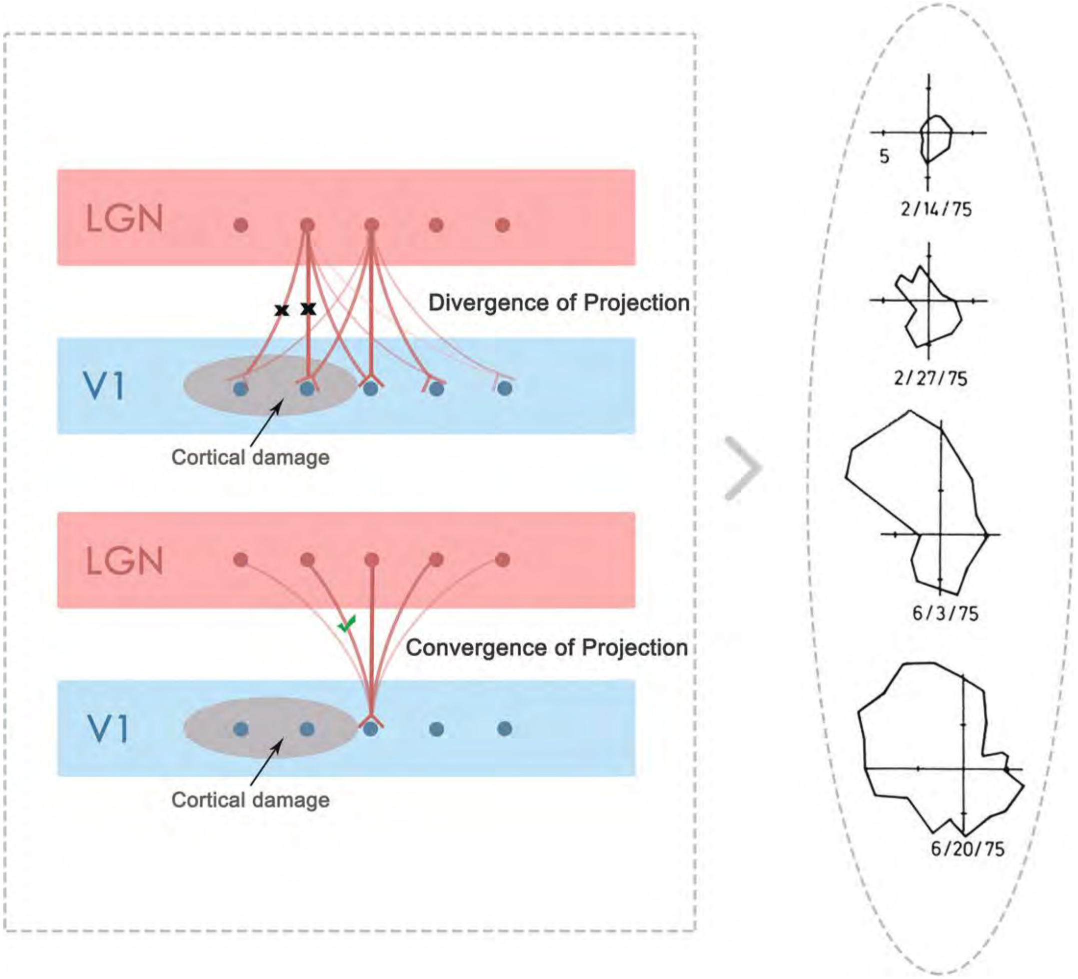

Figure 3. Visual field increase after regular visual training in patient H.H., who had suffered a bilateral occipital lobe infarction (panel on the right side). After a cortical injury as indicated by the dark ellipses (panel on the left side) some projections coming from the lateral geniculate nucleus (LGN) that have lost their primary projection at V1 still have some cortical representation in adjacent neurons because of divergence and convergence of projection. For details see text. (Figure abstracted from Pöppel et al., 1978.)

Another open question that has to be addressed, on the basis of observations with patient H.H. and other patients who showed some functional recovery, is how the topology of visual field representation within the recovered area is maintained or perhaps regained after an expansion of the functional visual field. If extended areas from the retina project to a circumscribed area of V1 (like a local column), these retinal areas necessarily lose their retinotopy because of convergence of projection. In spite of such local overlap of different retinal regions, retinotopy can be observed after recovery. This indicates that the retinotopy might either be re-gained by functional training or (in an ill-understood way) have never been lost. Also relevant is whether and how visual cortical neurons change their receptive fields after the recovery. For neurons adjacent to the damaged area, their receptive fields possibly expand due to the convergence of projection. Similar change, although in the opposite direction, can be speculated on the basis of divergence of projection for the cortical magnification factor within the recovered area. In the primate brain, receptive fields are reported to increase during the re-organization of the visual cortex after lesion, but the change might also involve intrinsic cortical interactions (Dreher, Burke, & Calford, 2001; Gilbert & Wiesel, 1992). However, the picture is less clear in the human brain. A full understanding of cortical re-organization after brain injury thus requires more case studies of patients using both behavioral and neurophysiological measurements.

The observations with patient H.H. lead to a further hypothesis concerning the mechanism of restitution of function that is open for experimental examinations. It might be suspected that a long-term improvement of function is obtained if within a short-term training session the performance level of a defined function is reduced (Figure 4). Short-term central fatigue, operationally defined here as a significant performance decrease toward the end of an experimental session lasting, for instance, for several hours, is hypothesized to trigger restorative mechanisms at the neural level by an increase of synaptic efficacy resulting in positive effects like the enlargement of the functional visual field (Figure 3). The depletion of neurotransmitters and their subsequent replenishment might trigger the neural mechanisms that result in the synaptic plasticity in this case. It can also be considered that there is a limit of improvement as visualized by the asymptotic upper limit beyond which no improvement can be expected within a defined neural population. This hypothesis about long-term improvement of functions based in short-term central fatigue can be explored with the use of real-time fMRI, and this hypothesis would apply to the entire repertoire of functions, not only to visual functions. The underlying idea is similar to a principle in physical training: In sports one has to go towards the limits in training, and only then a long-term improvement can be obtained. Of course, the brain is not a "muscle," but improvement in motor coordination is also not only "muscular." We assume that a fundamental principle is addressed with our hypothesis suggesting the necessity of central fatigue as the driving force for functional improvement. This idea, if confirmed by neurophysiological and neurochemical measurements, can help us to obtain deeper insight into the molecular and structural mechanisms of synaptic plasticity from a new perspective.

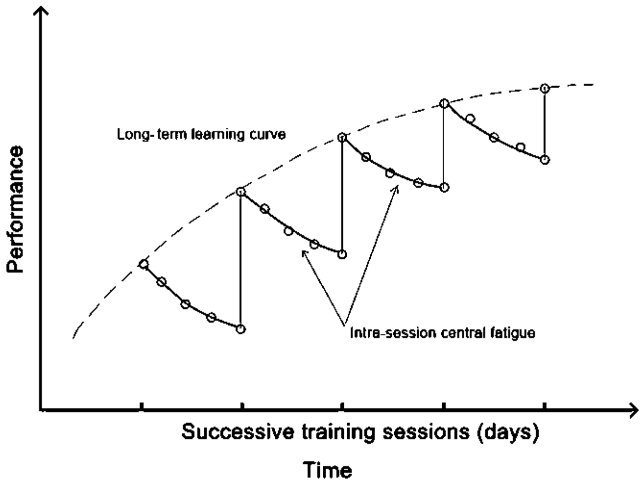

Figure 4. Hypothesis visualizing long-term effects of training: If within a short-term interval performance is reduced due to central fatigue, a long-term improvement of function is hypothesized to occur.

Sequential neural image creation in visual percepts

The bilateral injury affecting the visual cortex in patient H.H. also allowed us to obtain deeper insight into the temporal generation of visual percepts by using binocular rivalry as an experimental paradigm. When looking at horizontal red stripes and vertical green stripes through a red glass (left eye) and a green glass (right eye) as indicated by the two horizontal lines in front of the sketched head (Figure 5), subjects see sequentially for some seconds only the red and then for some seconds only the green stripes (e.g., Blake & Logothetis, 2002; Logothetis, 2008). This alteration of percepts can apparently not be suppressed voluntarily. Patient H.H. reports the same effect but with an extreme slowing when one percept is replaced by the previous one. This reversal is symbolized with the sequence of "clouds" shown on the right (Figure 5), which is derived from drawings by the patient. The replacement of vertically or horizontally oriented stripes is characterized by a gradual and oriented "pushing away" of one percept by the other. This gradual replacement of one percept by the other took tens of seconds, and it allows a direct view into the internal dynamics of visual processing. The slowing down can be used as a "functional microscope," and it suggests that the replacement of one perceived pattern by the other pattern is not a parallel process that occurs at all retinal positions simultaneously. It is a temporally dilated process that begins as a traveling wave (Lee, Blake, & Heeger, 2005; Wilson, Blake, & Lee, 2001) in one region of the visual field until the alternative percept is obtained. Across sessions, the "push" always starts from the left or right (when vertical lines serve as the pusher) or from the top or bottom (when horizontal lines serve as the pusher). If this "functional microscope" is reliable (and we believe it is), and the slowing down does not establish another neural algorithm (and we believe it does not), it can be argued that under normal circumstances, new percepts are created with a sequential neural mode; it is not a parallel process at all cortical positions simultaneously that operates in visual image creation. Furthermore, the observation of a

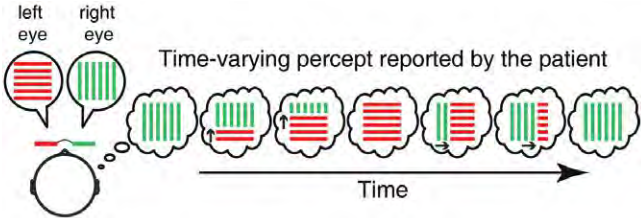

Figure 5. Time course of binocular rivalry reported by patient H.H., who suffered a bilateral occipital lobe lesion resulting in tunnel vision (Figure 3, panel on the right side).

retinotopically organized replacement with high precision from one percept to the other (Figure 5) suggests that V1 is the implementing structure for binocular rivalry.

Global rigidity and local plasticity in visual field representation

It is typical for single case studies with brain-injured patients that one cannot anticipate opportunities to study neural mechanisms, but one has sometimes the chance to "harvest serendipity." One such opportunity arose with patient H.P., who, as an adult, had suffered a stroke affecting the left visual cortex, and who had had a convergent squint in one eye since birth. In this patient, some details could be uncovered with respect to plasticity and rigidity of functional representation (Pöppel et al., 1987), although some essential questions remain unanswered. The visual fields of the two eyes were measured independently under photopic adaptation conditions (Figure 6). Shaded regions around the central white region represent areas of blindness. In the upper panel (right eye), the vertical meridian in the lower visual field is also the border of blindness. The blind spot (the small dark spot on the horizontal meridian at the right side) lies next to the area where acquired blindness begins. In the lower panel, the patient uses a pseudofovea in his squinting left eye for fixation, which lies next to the blind spot. The "vertical meridian" has been drawn through the position of the pseudofovea. Note that the area of blindness in the left eye is not limited with reference to the pseudofovea but with reference to the anatomical fovea, which is marked to the right of the blind spot with a dot at the horizontal meridian.

The special constellation of cortical scotoma and squint in one eye in this patient made it possible to test whether the oculomotor system uses the anatomical fovea or the pseudofovea to program the direction of saccadic eye movements. A visual stimulus was presented along the horizontal meridian between the projection of the anatomical fovea and the pseudofovea. The right eye in this experiment was covered with an opaque occluder. If under this experimental condition the patient looks to the left, he uses as a reference point the anatomical fovea; if he looks to the right, he uses the pseudofovea. The patient always looked right to visual targets with different eccentricities. This observation proves that the pseudofovea is used as a reference point for programming saccadic eye movements, thus, demonstrating plasticity of function in the oculomotor system of the squinting eye.

Although rigidity of visual field representation and plasticity in oculomotor programming could be shown in this

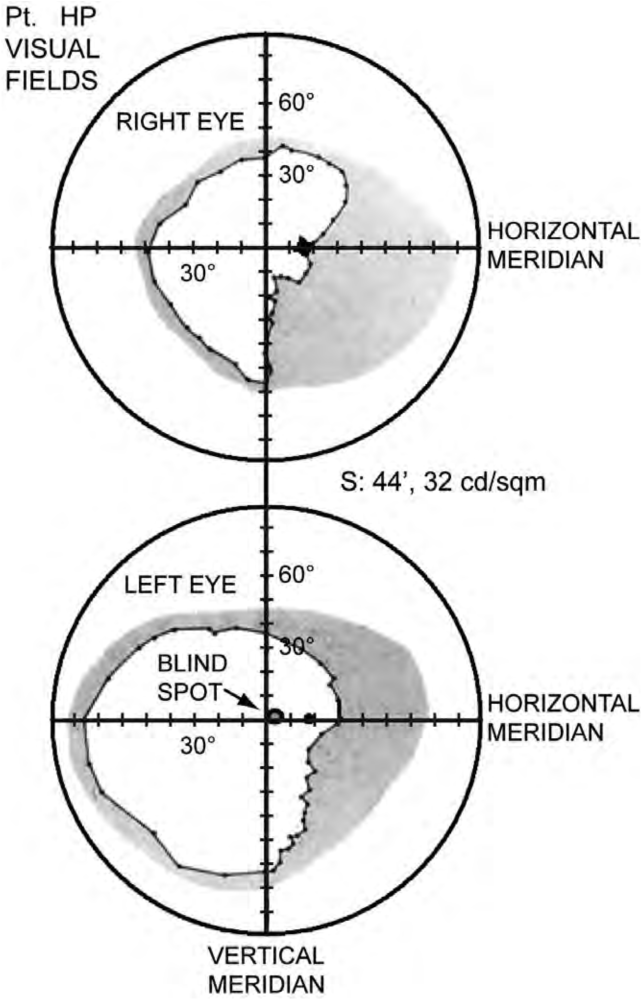

Figure 6. Visual field of the left and the right eye of patient H.P., who suffered an incomplete left occipital lobe lesion in adulthood in addition to a convergent squint of the left eye since birth. (Figure taken from Pöppel et al., 1987.)

case, and these results might have been anticipated at least with respect to the visual field representation (Rothschild & Mizrahi, 2015; Wandell & Winawer, 2011), there was one observation that appears to be rather paradoxical and which raises new questions. At the position of the blind spot in visual space of the squinting eye, the "good eye" showed a significant local decrease of sensitivity at the same position in visual space (Figure 7). This means that in spite of the rigidity of visual field representation at the visual cortex, local plasticity was also observed. The lack of visual input in one eye (the squinting eye) modulates the sensitivity for the same position in visual space for the other eye. Interestingly, this modulation is of an inhibitory nature, as sensitivity is reduced. How might it be possible to have both a rigid representation that is genetically determined and that remains unaffected for decades, and at the same time to have local plasticity? On the basis of the concept of divergence of projection, as referred to above, one can suspect that a modulation of local sensitivity far away from its primary target is possible. As the squint angle in this patient was some 17-deg visual angle, it can be concluded that at least up to such an angle of cortical representation of the visual field, divergence of projection may be observed. In this case (patient H.P.), as in the case with tunnel vision (patient H.H.), one is left, however, with the question as to how far one has to "travel" laterally across the visual cortex until one is no longer getting any direct input from a defined retinal area? One is furthermore confronted with the puzzle in patient H.P. as to whether this local inhibitory interaction for non-corresponding retinal points is of functional relevance.

Interhemispheric control of spatial attention at the midbrain level

It has been suggested previously that attentional control might be mediated by neural mechanisms already at the level of the superior colliculus in the midbrain (Singer et al., 1977). The involvement of the superior colliculus is an essential feature of a neural model explaining the eccentricity effect in attentional control, that is, the stronger inhibitory modulation of spatial attention for stimuli presented at the periphery relative to the perifoveal visual field is possibly mediated by the stronger representation of superior colliculus for peripheral stimuli via the retinotectal pathway (Bao & Pöppel, 2007). The potential participation of the superior colliculus has to be seen as complementary to neural mechanisms explaining selective attention at the cortical level, in particular in the parietal cortex (Behrmann, Geng, & Shomstein, 2004; Krauzlis, Lovejoy, & Zénon, 2013). Because of the limited spatial resolution of imaging technology as in fMRI (Logothetis, 2008), it still remains a technical challenge to demonstrate directly the involvement of the superior colliculus in eccentricity-dependent attentional tasks; thus, one has to rely on behavioral observations with patients (Pöppel & Richards, 1974) or on animal models (Sprague, 1966). How can the participation of attentional control on the collicular level be made

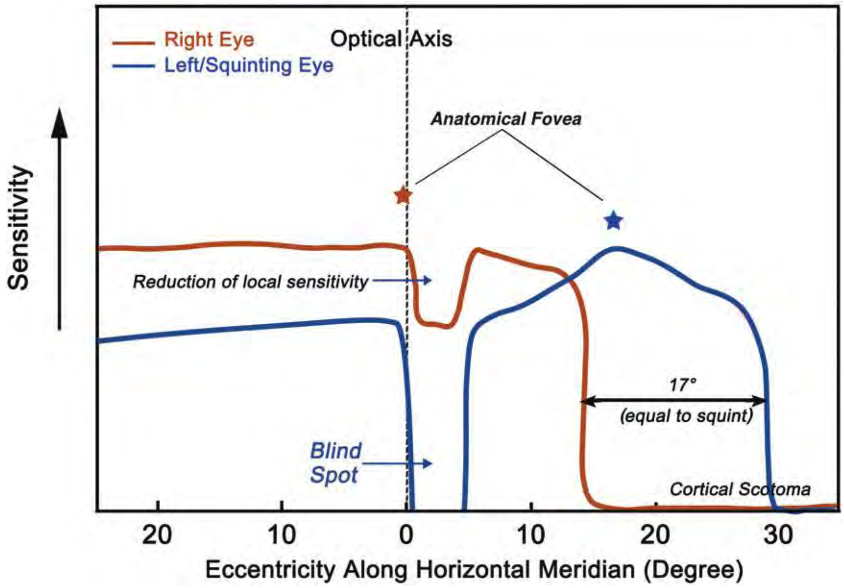

Figure 7. Increment threshold under photopic adaptation along the horizontal meridian in the foveal and perifoveal region for the right and left eye of patient H.P. (Figure 6). (Figure abstracted from Pöppel et al., 1987.)

plausible with a behavioral paradigm? It is suggested to be possible by employing habituation and facilitation of visual sensitivity and interhemispheric modulation of visual sensitivity (Figure 8). We describe a sequence of experiments with healthy subjects and patients who have suffered specific brain injuries, which support our hypothesis of a collicular mechanism, but which also raise new questions.

Continuous measurement of increment threshold for instance in the temporal visual field (TVF) of the left eye results in reduction of sensitivity, which is probably related to the Troxler effect (Troxler, 1804; Figure 8B, left column) in which an unchanging peripheral stimulus fades away and disappears if a steady fixation has been maintained for several seconds; this effect has been shown to have a central component reflecting habituation, and it is not based on local adaptation of receptors only (Hsieh & Tse, 2006). Spontaneous recovery to original values (Figure 8B, right column) takes approximately 20 min. In the second panel from the top, a phenomenon is described which suggests interhemispheric interactions. If after habituation of stimulating the TVF (Figure 8B, left column), stimulation is applied at a mirror-symmetric position in the nasal visual field (NVF; Figure 8B, middle column indicated with the red dot), sensitivity in the TVF is reset instantaneously to values prior to habituation (Figure 8B, right column) in contrast to a spontaneous recovery, which takes much longer.

In the third panel from the top in Figure 8, an equivalent experiment is described with a patient (E.K.) who has suffered a cortical injury in the left hemisphere resulting in a scotoma in the right visual field (Figure 8A, black area). In this patient, the same instantaneous resetting of sensitivity is observed, although the patient could not see the visual stimulus in his NVF of the left eye. In the bottom panel of Figure 8, a similar experiment is described with a patient who has suffered an optical tract injury (F.F.). This time the NVF is stimulated and a habituation is also observed. However, no such resetting of sensitivity can be triggered in this patient. Thus, the resetting of sensitivity after habituation is presumably mediated by midbrain mechanisms at the collicular level. These observations confirm on the behavioral level the model of attentional control as forwarded previously (Bao & Pöppel, 2007), but it still has to be documented by sufficiently sensitive technology as to whether this hypothesis will remain valid. Furthermore, it has to be clarified how the neural mechanisms at the suspected collicular level and the parietal cortex (Behrmann et al., 2004) interact.

Seeing with knowing: Conscious vision requires the primary visual cortex

Motivated by research on the visual system of the Syrian hamster (Schneider, 1969) and a case study in a monkey without a striate cortex (Humphrey, 1974), Pöppel, Held, and Frost (1973) investigated whether human patients who have suffered a brain injury resulting in blindness still exhibit some residual vision. This was in fact the case and this phenomenon has also become known as “blindsight” (Sanders, Warrington, Marshall, & Weiskrantz, 1974; Weiskrantz, Warrington, Sanders, & Marshall, 1974). Although initially being counter-intuitive and intensely criticized that one might deal perhaps with a stray-light effect (Campion, Latto, & Smith, 1983), blindsight has been confirmed by independent research groups: Patients with an acquired blindness due to cortical injuries affecting the visual cortex still process visual information, even though the patients are not consciously aware of the spared function (Perenin & Jeannerod, 1975; Stoerig, Hübner, & Pöppel, 1985; Torjussen, 1976; Zihl & Werth, 1984).

The discovery of residual vision has been made possible by detailed analyses of visual functions in single cases, such as patient A.W., who had suffered a stroke in the left hemisphere resulting in an incomplete hemianopsia in the right visual field of both eyes (Figure 9, black areas). The right upper quadrants were affected completely with some sparing of function in the right lower quadrants. Perimetric visual field measurements were repeated three times, indicating the temporal stability of the cortical scotoma. It can be noted that the area of blindness in the right lower quadrants is slightly larger in the left eye (NVF) compared to the right eye (TVF); this corresponds to observations referred to above (Engler et al., 1993) that retinal fibers from the nasal retina (TVF) may have a larger degree of divergence of a central projection resulting in slightly smaller areas of blindness.

Visual stimuli that were presented within the cortical scotoma in no case resulted in a conscious percept. However, when the patient was asked to look at “unseen” visual targets at different eccentricities along an oblique meridian within the right upper quadrant, the amplitude of saccadic eye movements correlated positively with target eccentricity. As the patient could not see the visual targets, the presentation of the visual stimulus was indicated by an auditory stimulus, which did not provide a spatial cue. The

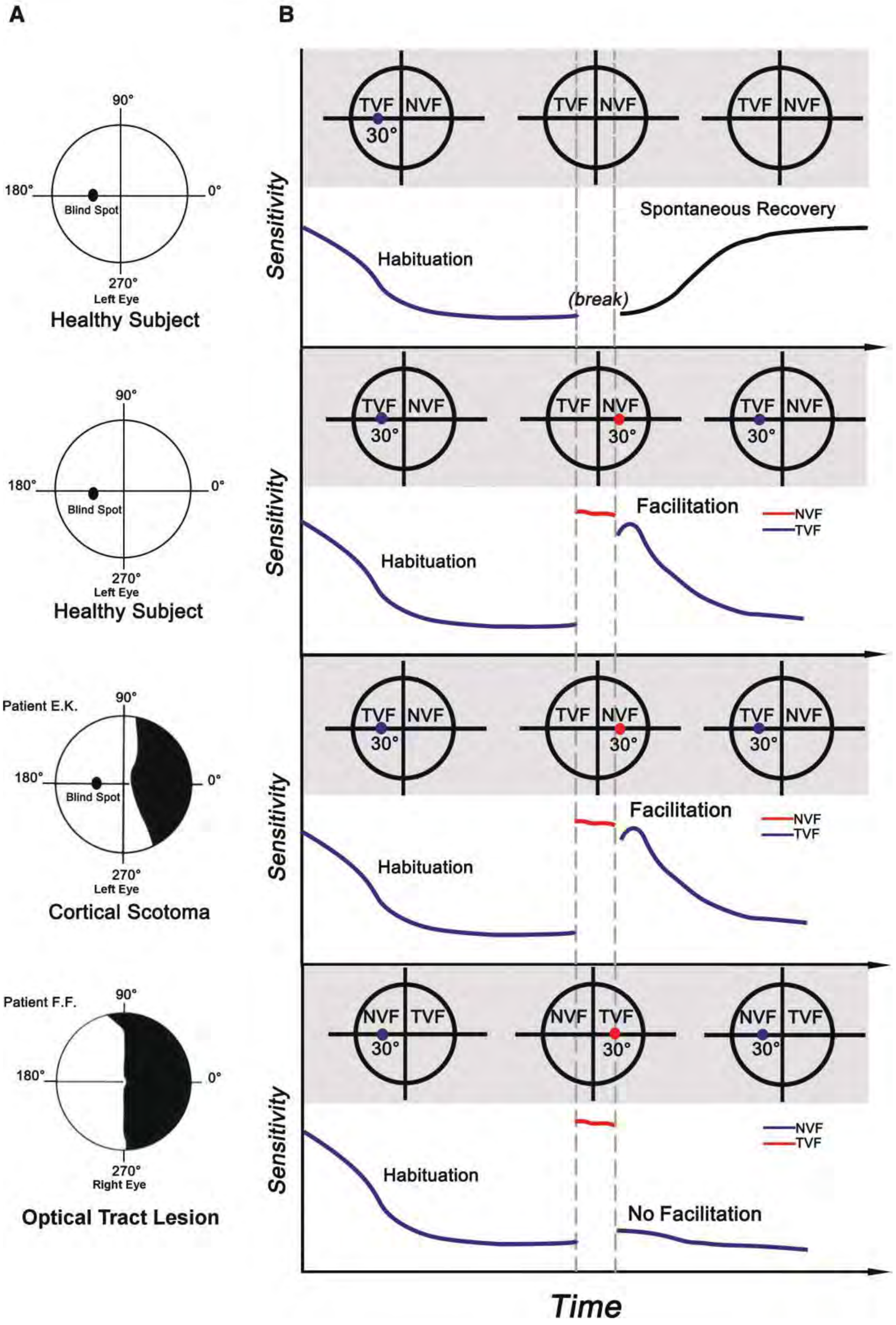

Figure 8. Interhemispheric modulation of visual processing as demonstrated with habituation and facilitation of local sensitivity. (A) Schematic illustration of tested eyes. (B) Different experimental conditions; for details see text. (Figure abstracted from Singer et al., 1977). NVF = nasal visual field; TVF = temporal visual field.

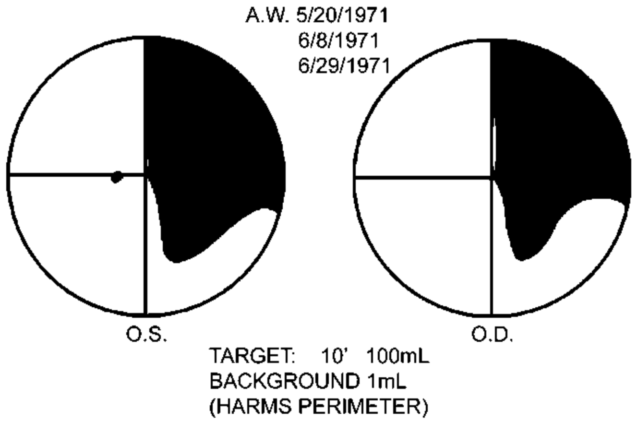

Figure 9. Visual field of patient A.W., who had suffered a stroke in the left hemisphere resulting in an incomplete hemianopsia in the right visual field of the two eyes (black areas); the right upper quadrants were affected completely with some sparing of function in the right lower quadrants. Perimetric visual field measurements were repeated three times indicating the stability of the cortical scotoma. (Referred to in Pöppel et al., 1973, Figure 1.)

experimental challenge in this case was to convince the patient to look at a visual stimulus he could not "see." This observation, together with those on detection and discrimination of visual stimuli using different experimental paradigms (Cowey, 2010) indicate that some visual processing is still possible on an implicit level (Pöppel & Bao, 2011). This capacity remains, however, undisclosed to the patients on an explicit level; residual vision or blindsight is characterized by "seeing without knowing." One may also refer to another relevant phenomenon of visual agnosia in which the recognition of objects is impaired following the damage of higher visual cortices in the extrastriate areas (Behrmann & Nishimura, 2010). However, the "seeing without knowing" in agnosia refers to the organizational and semantic levels (Funnell, 2000; Vecera & Gilds, 1998), unlike the blindsight, which loses "knowing" on the basic level of visual consciousness. In prosopagnosia (Damasio, Tranel, & Damasio, 1990), for instance, the perception of faceness is preserved while the recognition of specific faces (even one's own) is profoundly impaired. A more appropriate scenario can be proposed that the primary visual cortex serves as the source of all inputs for conscious perception and thus is the core and necessity, whereas the extrastriate cortices provide important decorations for the elaboration of visual inputs, thus contributing to visual recognition.

These observations in patients with circumscribed brain injuries strongly support the notion that the visual cortex is essential for conscious vision. We want to submit that "seeing without knowing" becomes "seeing with knowing" on this level of neural processing. Thus, the visual cortex is hypothesized to be located at a strategic crossroad. Information within the ascending visual pathway is characterized by "seeing without knowing" as exemplified by the observations on brightness constancy throughout the visual field or color induction. This mode of "seeing" represents logistical functions (Pöppel, 1989) that are necessary but not sufficient functions for visual percepts on a conscious level. The information from the visual cortex is sent to a large number of extrastriate areas and beyond, and many of these areas project back to V1 (Felleman & Van Essen, 1991). These extrastriate areas independently do not mediate conscious vision, as is demonstrated by patients with lesions in the optic radiation (e.g., Stoerig et al., 1998). Of course, a full emergence of conscious experience with various properties requires the involvement of extrastriate areas and their interactions with the primary and other brain cortices. Thus, we are left with the conclusion, at the very basic conscious level, that the striate cortex mediates "seeing with knowing."

Necessary but not sufficient conditions for visual perception: A final remark

In a taxonomy of function (Pöppel, 1989), content or "what-functions" (like percepts in the different sensory modalities, or memories in the semantic or episodic mnemonic systems) has been distinguished from logistical "how-functions" (like attentional control, activation of functions as modulated, for instance, by the circadian clock, or temporal organization of distributed neural activities). Logistical functions are necessary for the representation of content functions; a breakdown in the temporal machinery of the brain, a failure in attentional control, or switching off the activation system, results in a severe disruption or loss of perceptual or mnemonic content. As we show in our analyses of visual processing, the concept of logistical functions and its distinction from content functions also applies to the early visual pathway.

In the perception of objects, homogeneity of brightness of perceptual surfaces is implicitly assumed and taken for granted; it is usually not even questioned that it could be otherwise, because the spatial distribution of threshold sensitivity under photopic conditions would predict an inhomogeneous brightness distribution (Figure 1). As we argue, both constancy of brightness throughout the visual field and a functional equilibrium between the different color channels (Figure 2) are already implemented at the retinal level. It is suggested that this processing in the early visual pathway is a necessary condition for visual perception and results at later stages in effortless recognition of visual objects.

Although the value of single case studies in patients with circumscribed lesions of the brain is sometimes questioned, we want to submit on the basis of our analyses that the unique patterns of neural systems after injury can lead to new insights into the stream of information processing prior to those neural mechanisms that are responsible for distinct percepts. On that basis, we can refer to early processing stages as "pre-semantic" and that they represent logistical functions of the brain. Furthermore, we can extract hypotheses about neuroanatomical characteristics; as we suggest, recovery of function (Figure 3) implies a special mode of retinofugal projection with a high degree of divergence in central representation, and correspondingly a substantial amount of convergence onto local neural nets. For recovery of function (which is a special mode of visual learning), we suggest as a neural mechanism short-term fatigue, which results in long-term functional improvement (Figure 4). However, what remains an enigma is how it is possible that, after functional recovery as seen in the enlargement of the visual field, the topological relations between local stimuli are maintained. In spite of the pre-wired representation of the visual field at the cortical level (Figure 6), it comes as a surprise that there are also local interactions for non-corresponding retinal points of the two eyes (Figure 7); this paradoxical observation may be explained on the basis of a substantial degree of divergence of projection (Figure 3) at the cortical surface allowing the establishment of new local interactions.

Single-case studies are often characterized by surprising observations that are not and cannot be anticipated. In one patient, we observed an extreme slowing down in binocular rivalry (Figure 5); this effect we use as a "temporal microscope." If we deal in this case with only a slowing down in neural processing, and if we do not have to assume (as we do) the implementation of an alternative neural strategy triggered by the lesion, it can be argued or at least speculated that the build-up of a visual percept is not an instantaneous and parallel process within a neural structure, but that it is a fast sequential process sweeping across the participating neural elements as in technological systems.

Although for control of visual attention, cortical mechanisms have been demonstrated with advanced imaging technologies, we present in our analyses cases that clearly indicate the participation of sub-cortical structures (Figure 8). Inter-hemispheric inhibitory mechanisms presumably at the level of the superior colliculus of the midbrain are suggested to be involved in spatial attention; thus, cortical and sub-cortical mechanisms are involved in a complementary way. In particular, the "eccentricity effect" of spatial attention (Bao & Pöppel, 2007) suggests different attentional mechanisms for the perifoveal and peripheral regions of the visual field, which are related to different retinocentral projection systems.

It is of course a trivial statement that different extrastriate areas are responsible for the richness of our visual percepts, and that these structures, together with others at the cortical mantle, provide the sufficient conditions for object and scene perception. We claim that the visual cortex (area 17, V1) is the one and only structure that is essential for conscious vision. If the integrity of the primary visual cortex is disrupted, if it does not receive direct geniculate input, there is no longer conscious vision (Figure 9). We cannot find evidence that contradicts this statement.

Disclosure of conflict of interest

The authors declare that there are no conflicts of interest.

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SHORT REPORT

Spatial orienting around the fovea: exogenous and endogenous cueing effects

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Abstract The effect of covert attention in perifoveal and peripheral locations has been studied extensively. However, it is less clear whether attention operates similarly in the foveal area itself. The present study aims to investigate whether the attentional orienting elicited by an exogenous or endogenous cue can operate within the foveal area and whether attentional orienting operates similarly between foveal and perifoveal regions. By manipulating exogenous orienting in Experiment 1 and endogenous orienting in Experiment 2, we observed both forms of cueing in the foveal area. Specifically, we observed a larger exogenous cue-induced inhibitory effect (i.e., inhibition of return effect) and a similar endogenous cue-elicited facilitatory effect for the perifoveal relative to the foveal targets. We conclude that exogenous and endogenous orienting subject to two independent attentional systems with distinct modulation patterns in the foveal area.

Keywords Foveal processing · Eccentricity effect · Endogenous attention · Exogenous attention

Introduction

Orienting attention toward specific locations covertly, without any change in gaze direction, has been shown to improve stimulus detection and discrimination in the cued location compared with an uncued control condition (Posner 1980). Furthermore, attention could be oriented either exogenously and reflexively, using a spatially non-predictive peripheral cue, or endogenously and voluntarily, using a predictive central symbolic cue (Chica et al. 2013; Klein 2009). Exogenous attention produces a biphasic response pattern denoted by facilitation at short cue-target interval (<200 ms) and inhibition of return (IOR) at longer intervals, which presumably reflects a bias against reorienting attention to a location that has been previously attended (Klein 2000). The effects of endogenous cues usually show a comparatively delayed buildup of facilitation peaking at 300 ms and then remain for a longer duration (Müller and Rabbitt 1989). It has been considered as a voluntary system that corresponds to our ability to voluntarily monitor information at a given location.

Given that the properties of visual processing vary widely across the visual field (Pöppel and Harvey 1973; Strasburger et al. 2011), it might be possible that spatial cuing effects also differ for different visual regions. Some recent studies suggest that attentional orienting as studied with the paradigm of IOR exhibits a functional dissociation in the visual field, with larger inhibitory effects at periheral (21°) relative to perifoveal (7°) regions (Bao and Pöppel 2007; Bao et al. 2012). This eccentricity effect of IOR is independent of cortical magnification factor (Bao et al. 2013) and resistant to subjects' practice (Bao et al. 2011). These observations suggest different modes for modulating stimulus processing in the perifovea compared to the periphery of the visual field. An unanswered question,

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however, is whether attentional orienting also operates inhomogeneously between our most effective system for achieving high-resolution visual perception, i.e., foveal processing, and the relatively lower-resolution perifoveal vision. Attention allows to select locations around the fovea, i.e., the central 2° of the retina (Lavidor and Walsh 2004). During active fixation when stimuli are presented to the fovea, there is a strong incentive to hold attention at the central location. From an evolutionary perspective, one might expect that in this case, the shift of attention toward incoming cues and targets around the fovea is not necessary, since attention is already allocated to the fovea while maintaining fixation. The aim of the present study is to examine whether attentional orienting elicited by an exogenous or endogenous cue operates differently in the foveal and perifoveal visual field. Specifically, we conducted two experiments with Experiment 1 using an exogenous cue and Experiment 2 using an endogenous cue.

Experiment 1

Methods

Participants

Nine right-handed students (three males, 20–25 years old) from Peking University (PKU) participated in the study after giving informed written consent. All had normal or corrected-to-normal vision, and all were naïve to the purpose of the experiment.

Apparatus

Visual stimuli were generated using MATLAB 7.13 in conjunction with the Psychophysics Toolbox (Brainard 1997) and displayed on a 19-in CRT monitor (1024 × 768 resolution, 100 Hz refresh rate). The visual distance was 57 cm. Responses were collected through a keyboard.

Materials and procedure

Each trial started with a white cross subtending 0.2° visual angle presented at the center of a dark computer screen. Participants were instructed to keep fixation on the cross throughout the experiment. After 500 ms, a white outline box serving as the exogenous cue subtended a 0.4° visual angle and appeared for 100 ms at 1° or 7° to the left or right of the center. Following a 70 ms inter-stimuli interval (ISI), the same outline box appeared at the center surrounding the fixation cross for 100 ms. After another interval of 70 ms, a white solid circle (0.3°) serving as a target appeared at either the cued location or the uncued opposite location with the same eccentricity (see Fig. 1, left). Participants were required to press a response key as soon as they saw the target while maintaining fixation. On catch trials, only the cue was presented and participants were to withhold key pressing.

There were 384 target trials and 96 catch trials. All trials were completely randomized and arranged into six blocks with 80 trials in each block. The number of trials for targets appearing in the left or right visual field and at 1° or 7° eccentricity was balanced in both cued and uncued conditions.

Data analysis

The total error rate for each subject was lower than 2 %. Correct reaction times (RTs) for each subject were first submitted to descriptive statistics, and the RTs beyond 3 standard deviations were considered as outliers and excluded. Anticipations (<100 ms) and retardations (>800 ms)

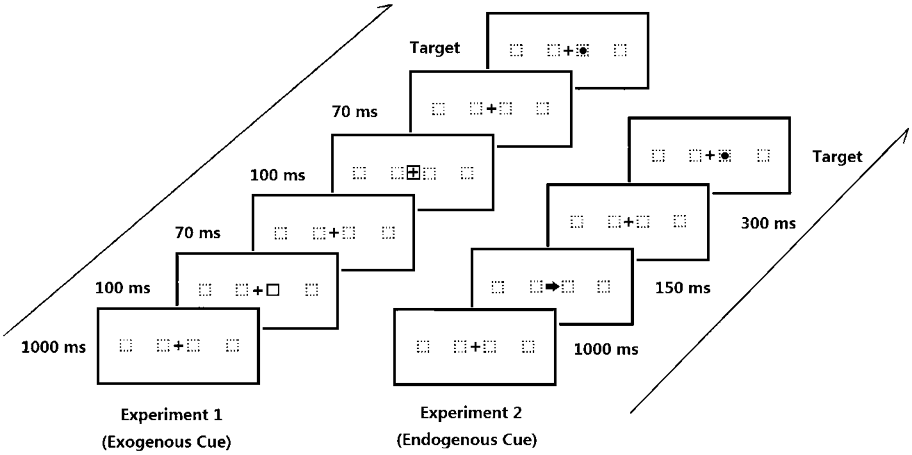

Fig. 1 Sample trial sequence of Experiment 1 (exogenous cue) and Experiment 2 (endogenous cue). In this example, the target is presented in the cued location at 1° eccentricity

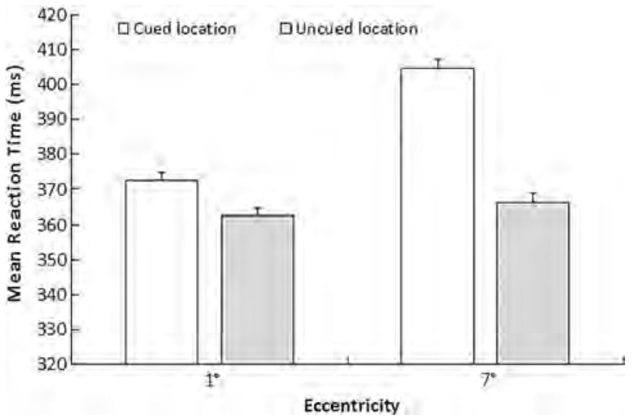

Fig. 2 Reaction times as a function of target location (cued vs. uncued) and stimulus eccentricity (1° vs. 7°) in Experiment 1. Larger IOR effect (RT difference between cued and uncued trials) was observed for 7° relative to 1° stimulus eccentricity. Within-subject error bars is calculated for each condition using Cousineau (2005)

were further employed to exclude RTs. An analysis of variance (ANOVA) with target location (cued location, uncued location) and stimulus eccentricity (1°, 7°) as within-subjects factors was conducted on the mean RT data.

Results

The ANOVA revealed a main effect of target location $[F(1,8) = 56.17, p < 0.001, \eta_p^2 = 0.88]$, with a longer RT of cued trials than that of uncued trials, indicating an IOR effect (Fig. 2). The main effect of eccentricity was significant $[F(1,8) = 7.11, p < 0.05, \eta_p^2 = 0.47]$, revealing a slower RT for perifoveal locations. Furthermore, the eccentricity effect significantly interacted with target location $[F(1,8) = 105.42, p < 0.001, \eta_p^2 = 0.93]$. Further paired t test for the IOR magnitude ($\text{IOR} = \text{RT}_{\text{cued}} - \text{RT}_{\text{uncued}}$) at 1° and 7° indicated that the latter was significantly larger (10 vs. 38 ms on average, $p < 0.001$).

Experiment 2

Methods

Participants

Nine students (five males) aged from 19 to 25 from PKU participated in Experiment 2. All of them were right-handed and had normal or corrected-to-normal vision.

Apparatus, materials and procedure

The apparatus were identical to the one used in Experiment 1. The initial display consisted of a 0.2° white fixation cross at the center against a black background. After 500 ms, an arrow subtending 0.4° by 0.3° visual angle appeared centrally for 150 ms, pointing to the left or right. Participants were explicitly informed that the cue was predictive. After a 300 ms ISI, the target was likely to appear in the direction of the arrow on 80 % of the trials, measuring 1° or 7° eccentricities, whereas it could appear at the opposite location on 20 % of the trials (see Fig. 1, right). Participants were required to keep their fixation at the cross throughout each trial and detect the targets as quickly and as accurately as possible.

There are 576 trials in total (384 valid, 96 invalid and 96 catch trials) and were divided into six blocks. Among the 480 target trials, targets were presented at 1° and 7° equally. The 96 catch trials were mixed with the other target trials in a random sequence.

Results

All participants' mean RTs were analyzed with a repeated-measure ANOVA with target location (cued location, uncued location) and stimulus eccentricity (1°, 7°) as two independent variables. RTs were faster for cued targets independent of whether they were presented at the foveal or perifoveal location (see Fig. 3). This was confirmed in the ANOVA results which showed a main effect of target location $([F(1,8) = 12.11, p < 0.01, \eta_p^2 = 0.60])$, but no main effect of eccentricity $([F(1,8) = 2.66, p = 0.14, \eta_p^2 = 0.25])$ or the target location × eccentricity interaction $([F(1,8) = 0.25, p = 0.63, \eta_p^2 = 0.03])$.

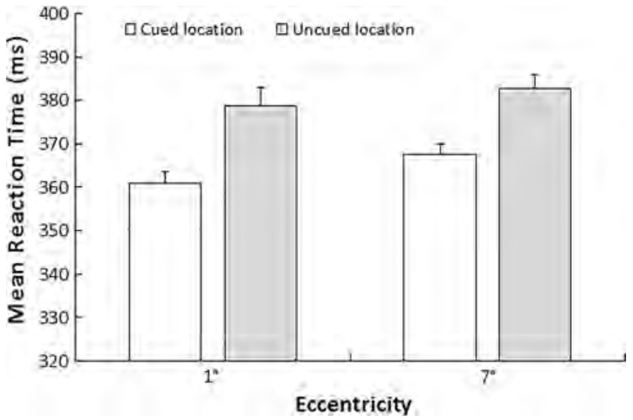

Fig. 3 RT as a function of target location and stimulus eccentricity in Experiment 2. Endogenous cuing effects (RT difference between uncued and cued trials) are not different between 1° and 7° eccentricities. Within-subject *error bars* is calculated for each condition using Cousineau (2005)

Discussion

In the present study, effects of both forms of cueing (exogenous and endogenous) within the foveal area were observed. When cues and targets were presented close to the fovea during active fixation, as had been done in Experiment 1, RTs were significantly longer for cued than for uncued foveal targets, indicating an IOR effect. However, spatial cues can also lead to an apparent facilitation effect in the foveal region, with shorter RTs for cued relative to uncued targets as observed in Experiment 2. It appeared therefore that spatial cues engendered both facilitatory and inhibitory effects at the fovea, even though this region was continuously fixated and continuously attended. Thus, processing of foveal stimuli can be further influenced by spatial attention, i.e., above the inherent advantage conferred by foveation of stimuli, the processing of such stimuli can additionally be affected by spatial attention. This observation contradicts our prediction that no attentional modulation should be observed within the foveal area. The reason for this unexpected effect could be that the presence of rapidly changing and discrete stimuli to the fovea presents an unusual experimental situation which rarely occurs outside the laboratory. Under natural settings, the visual and attention systems rely heavily upon organization of visual scenes. As long as the eyes focus directly on an object or part of an object, attention should be restricted to the spatial region within the object's boundaries, and the shift of attention should hardly occur in the foveal area. Presumably, the inclusion of foveal cues and targets in a setting close to natural viewing conditions will furnish information that cannot be obtained with experiments which do not mimic ecological situations.

In spite of these limitations, the two experiments provided important information. In Experiment 1, we observed a robust eccentricity effect of IOR, i.e., a stronger IOR magnitude for the perifovea (7°) relative to the foveal area (1°), showing a different cue-induced modulation of detection RTs between these two regions. This indicates that the interaction between target location and eccentricity is not limited to perifoveal and peripheral regions, as shown in previous studies (e.g., Bao and Pöppel 2007), but can also be extended to the foveal and perifoveal visual field. This might be related to the non-uniform distribution of photoreceptors in the retina and the structural characteristics of the visual cortex and other features of the retinocortical pathway (cf. Handy and Khoe 2005). The present finding is thus consistent with the hypothesis that attentional control may operate differentially between foveal and perifoveal visual processing.

We found from Experiment 2 that unlike exogenous attention, directing endogenous attention via central informative cues to the target location reduced RTs both at foveal and perifoveal cued locations, and the cuing effects were independent of stimulus eccentricities. These different results might be due to the more flexible nature of endogenous attention in comparison with exogenous attention. As has been shown in previous studies, the shift of attention induced by an exogenous cue is more resistant to interference and can occur even when the cue is non-predictive (Chica et al. 2013). Compared to exogenous attention, endogenous attention is a more adaptive mechanism. When participants see an arrow indicating the likely side (i.e., left or right) along the horizontal meridian for an upcoming target, but are not told whether the target will appear at a foveal or perifoveal location, they can efficiently control and allocate attentional resources and uniformly prepare for the foveal and perifoveal target stimuli. The differences between exogenous and endogenous orienting may be due to the fact that endogenous attention is cortical in nature, while exogenous attention is mediated by both cortical and subcortical networks (Corbetta and Shulman 2002). In the present study, we found yet another differential aspect between endogenous and exogenous attention via comparing the cueing effects at foveal and perifoveal regions of the visual field.

In conclusion, selective allocation of visual attention can operate in the immediate vicinity of the fovea. Although the present study is not the first one to show an influence of spatial attention on foveal processing, our data provide the first behavioral evidence of different inhibitory processing induced by exogenous orienting and similar facilitatory processing elicited by endogenous orienting at foveal and perifoveal regions. These observations suggest that attentional orienting initiated by exogenous and endogenous cues have to be considered as two different processes, with distinct modulation patterns in the visual field.

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PLOS ONE

RESEARCH ARTICLE

Attentional modulation of speed-change perception in the perifoveal and near-peripheral visual field

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Abstract

The ability to perceive changes in motion, such as rapid changes of speed, has important ecological significance. We show that exogenous and endogenous attention have different effects on speed-change perception and operate differently in different regions of the visual field. Using a spatial-cueing paradigm, with either exogenous or endogenous cues followed by drifting Gabor patches of changing speed that appear at the cued or uncued location, we measured participants' thresholds for localizing both acceleration and deceleration of the Gabor patches in different regions (5˚ and 10˚) of the visual field. The results revealed a larger exogenous cueing effect, indexed by a lower threshold for the cued relative to the uncued conditions, at 5˚ for perceiving acceleration and at 10˚ for perceiving deceleration. Endogenous attention, in contrast, improved performance equally at both eccentricities. We conclude that exogenous and endogenous spatial orienting constitute two independent attentional systems, with distinct modulation patterns on speed change perception in the visual field. While exogenous attentional modulation is eccentricity-dependent, endogenous attention acts homogeneously in perifoveal and near-peripheral regions of the visual field.

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Introduction

The role of covert spatial attention (i.e., the focusing of attention on a peripheral location without change in gaze) has been well examined in a variety of visual tasks. Spatial attention allows selective prioritization of stimulus processing at a given location, and selectively enhances, amongst others, contrast sensitivity, spatial resolution, reaction time, two-pulse resolution, and processing speed for stimuli at the attended location [1,2,3,4,5]. Besides effects of attention on static stimulus properties, there is evidence that spatial attention also plays a role in the perception of aspects of visual motion, such as motion coherence and the speed or the size of moving stimuli [6,7,8]. These studies have mainly focused on how we perceive constant motion, however, motion change, i.e., acceleration and deceleration, has not yet been studied in detail. Given that objects under ecological conditions rarely move at constant speed, the

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ability to detect changes in our ever-changing environment is an important challenge for the human visual system, e.g. perceiving transient changes of the speed of a moving object in a specific direction to avoid collision. One goal of the present study, therefore, is to explore the effects of spatial attention on speed-change perception.

A sudden increase or decrease in speed represents an abrupt stimulus change and as such resembles a stimulus onset or offset, where neurons typically respond by an increase or decrease in firing rate [9]. However, unlike stimulus onset or offset, speed changes may require integrating and comparing speed information over time. Thus, processes that mediate responding to a stimulus change may differ from those for the response to stimulus onsets. In addition, there is, (to the best of our knowledge), no unequivocal clear evidence as to whether the brain has a direct representation of the extent of stimulus acceleration or deceleration [10,11,12]. Even though single neurons in area MT apparently encode motion attributes like the motion's direction and the speed of a moving target, and the neurons' activity pattern are correlated with behavioral performance during motion detection and discrimination [13,14,15], a similar cellular mechanism for coding acceleration and deceleration apparently does not exist; single neurons in area MT do not seem to be sensitive to acceleration. Alternatively, population pooling of neuronal responses could be a process underlying the representation of changes, and in particular speed changes over time [16,17,18]. Furthermore, considering the aforementioned studies which show that spatial attention enhances several aspects of visual processing, it is worthwhile to determine whether the mechanisms that are possibly responsible for acceleration and deceleration could be modulated by spatial attention.

It has been well-established that covert spatial attention can be uncoupled from gaze [19] often described with the spotlight metaphor [20], and it has been hypothesized since Wilhelm Wundt [21] more than a hundred years ago that there are at least two ways of allocating spatial attention. On the one hand, observers can voluntarily deploy attention to the spatial location that is relevant for a current task. On the other hand, physically salient stimuli can involuntarily capture attention, even when they are unrelated to the current goal-directed task. In the spatial cueing paradigms developed by Eriksen and Posner and colleagues [20,22,23,24] spatial attention can be either attracted exogenously and reflexively, using a spatially non-predictive peripheral cue, or directed endogenously and voluntarily, using a spatially predictive central symbolic cue. Similar distinctions have been conceptualized as automatic vs. voluntary attention [25] or transient vs. sustained attention [26]. Attentional modulation of performance typically differs depending on the type of spatial attention deployed [25,26,27,28,29] (see [1] for review). Thus, the present research asks further whether and how these two types of attention affect speed-change perception.

It has become increasingly evident that attentional effects also show functional differences in different regions of the visual field. That might not come as a surprise in light of the fact that perceptual performance shows essential inhomogeneities in the visual field [30,31] most notably between the central region and the more peripheral visual field (see [32] for review). Using a spatial cueing paradigm with inhibition of return (IOR, the inhibitory process setting-in approximately 300 ms after the initial visual orienting at the cued location; cf. [33,34]), Bao and colleagues found in a series of studies that spatial-cueing effects varied as a function of stimulus eccentricity; more specifically, the inhibitory component of attentional control, indexed by the magnitude of IOR, is much stronger at the periphery than the perifoveal region suggesting different processing mechanisms for perifoveal and peripheral stimuli [35,36,37,38]. This eccentricity effect is further found to be independent of cortical magnification [39] and it is resistant to subjects' practice [40]. These findings provide support for the hypothesis that attentional modulation in the visual field is not homogeneous. Therefore, it is reasonable to hypothesize that attentional control also operates differently on speed-change perception in different regions of the visual field.

In the experiments presented here, we examined the possible attentional modulation of both exogenous and endogenous attention in a speed-change detection task where targets were presented in different regions of the visual field. It was expected that shifting attention to a specific spatial location would affect the detection of a sudden speed change of moving stimuli at that location. Given the inhomogeneity of attentional control in the visual filed, it was further anticipated that the attentional modulation on speed-change detection would depend on the eccentricity at which the target appears. In Experiment 1, thresholds for localizing both acceleration and deceleration of drifting Gabor patches were measured using a peripheral cueing paradigm in which the Gabor patches that changed speed could appear at two eccentric (5° or 10°), cued or uncued locations. Experiment 2 was designed to investigate whether endogenous attention would affect speed-change perception, and if so, whether its effect would be similar to that of exogenous attention.

Materials and methods

Participants

Thirty-six healthy right-handed students from Peking University (aged 18–28 years) participated in the study (Exp 1: 16 participants, 7 males; Exp 2: 20 participants, 10 males). All participants had normal or corrected-to-normal vision, and all were naïve with respect to the purpose of the experiment. All participants gave written informed consent before the experiments and they received moderate rewards for their participation. The experiments had been approved by the Committee for Protecting Human and Animal Subjects in the School of Psychological and Cognitive Sciences at Peking University and were in accordance with the Declaration of Helsinki.

Apparatus

Visual stimuli were generated using MATLAB 7.13 (MathWorks, Natick, MA) in conjunction with the Cogent toolbox (http://www.vislab.ucl.ac.uk/Cogent/) and displayed on a gamma-corrected 20-in CRT monitor with 1024×768 resolution at a refresh rate of 100 Hz. Responses were collected on a keyboard.

Materials

In both experiments, stimuli consisted of two diagonally oriented Gabor patches (45° or 135° orientation, spatial frequency:1 cyc/deg, Gaussian envelope in cosine phase with $\sigma = 0.75°$, corresponding to a visible grating diameter of ~ 4.5°; Michelson contrast 99.8%; background luminance 20 cd/m^2), with its grating moving behind the Gaussian aperture orthogonally to their respective orientation, either up-right or up-left. Motion, and motion direction, were clearly visible at all tested conditions. The fixation mark was a white cross subtending 0.8° visual angle. In Exp 1, the spatial cue for attracting exogenous attention was a white dot, presented at 5° or 10° eccentricity to the left or right of the center and subtending 1° visual angle. For Exp 2, a white 0.8°×0.6° arrow, presented in the center of the computer screen, served as endogenous cue.

Procedure

The experiment took place in a dimly lit room. Subjects were seated at 57 cm distance from a computer screen, with viewing distance kept constant by using an adjustable head-chin rest. The stimulus sequence in a trial is illustrated in Fig 1. Each trial started with the presentation of

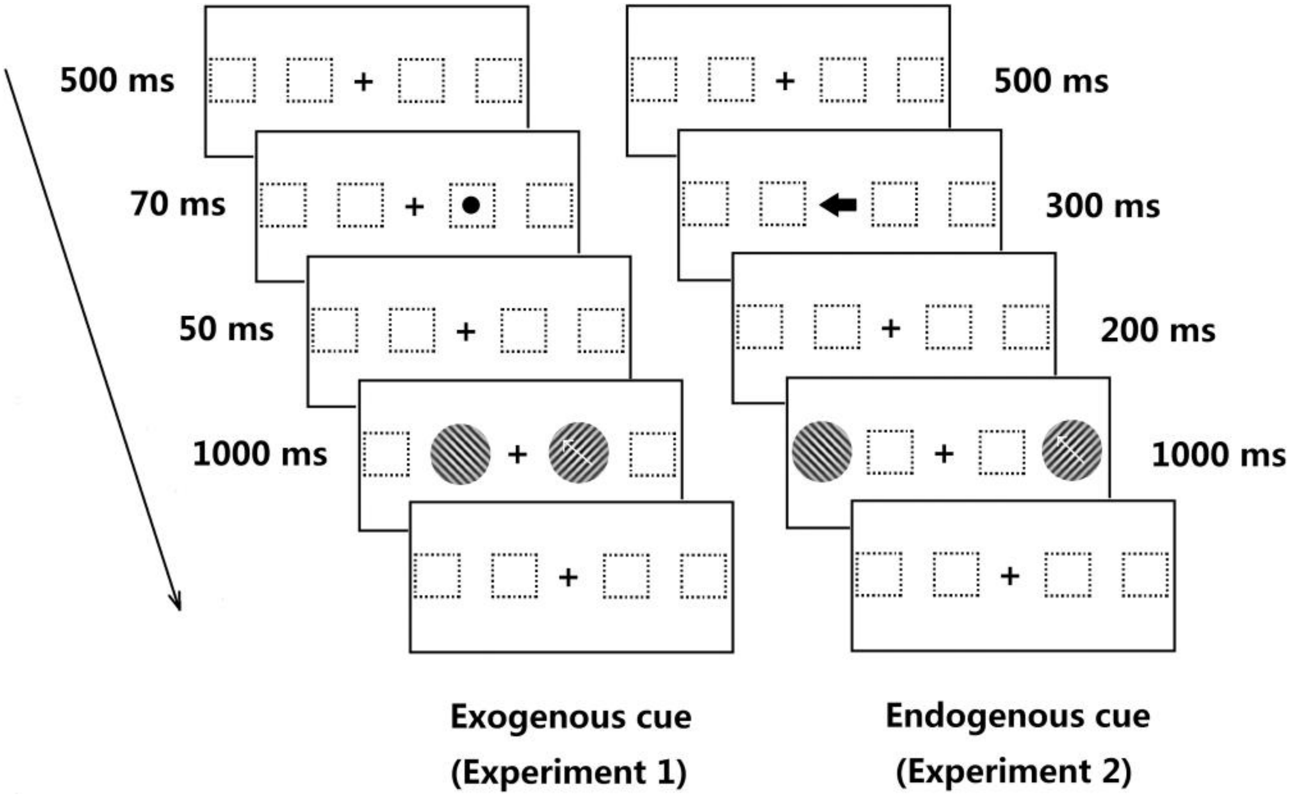

Fig 1. Sample trial sequences in Exp 1 (exogenous cue; left) and Exp 2 (endogenous cue; right). In this example, the target is presented in the cued location at 5˚ eccentricity (Exp 1) and in the uncued location at 10˚ (Exp 2).

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a fixation point for 500 ms at the center of the screen. In Exp 1, the exogenous cue appeared for 70 ms left or right of the fixation point (50% validity, non-informative) at an eccentricity of either 5˚ or 10˚. An inter-stimulus interval (ISI) of 50 ms followed the cue offset. This interval was chosen short enough to prevent goal-directed saccades. In Exp 2, the endogenous cue was a single arrow pointing either to the left or to the right, indicating the likely location of the changing-speed target (75% validity; that is, the target appeared in the direction of the arrow on 75% of the trials). After the offset of the spatial cue (exogenous or endogenous) and the corresponding ISI, two drifting Gabor patches with a base speed of 6 deg/s were presented, one to the left and one to the right of fixation on the horizontal meridian, at either 5˚ or 10˚ of eccentricity. After a fixed-speed period of 500 ms, one Gabor patch abruptly changed its speed, after which the stimulus moved constantly at one of six different test speeds (plus a control) for another 500 ms while the other Gabor patch continued to move at the base speed of 6 deg/s. Speed changes of 0%, ±10%, ±20%, ±30%, ±40%, ±50%, and ±60% relative to the base speed were used; for example, 20% acceleration for 6 deg/s base speed resulted in 7.2 deg/s speed, and 20% deceleration in 5 deg/s speed. Participants were asked to maintain fixation throughout the trial sequence and to indicate, by pressing one of the two keyboard buttons, whether the right or the left stimulus changed its speed. A training phase with neutral-cue trials preceded the experiments.

Design

The sign of the speed change, i.e., acceleration vs. deceleration, was designed as a between-subject factor; half of the subjects participated in the acceleration condition (8 in Exp 1, and 10 in

Exp 2) and the other half in the deceleration condition. In Exp 1, all the other conditions (stimulus eccentricity, left/right visual field, and cue validity) were within-subject factors and were used equiprobably with each of the six speed steps. The resulting 48 different trials (6 speed steps × 2 left/right visual field × 2 eccentricities × 2 cue validities) were repeated 20 times in randomized order, for a total of 960 trials for each subject. In Exp 2, there were 1152 trials for each subject, divided into 24 blocks of 48 trials, of which 36 trials were valid (target appeared at the cued location), and the remaining 12 were invalid. In both experiments, the two eccentricity conditions (5° and 10°) were completed in different sessions and on different days. The condition order was randomized and counterbalanced across participants, i.e. half of the participants performed the 5° condition first, and the other half the 10° condition first.

Data analysis

Speed-change detection thresholds were obtained by the method of constant stimuli. Psychometric functions were fitted using the Palamedes toolbox for MATLAB [41,42], which implements maximum-likelihood estimation. We fitted the psychometric function with a Weibull function:

$$\mathrm{p_c} = 1 - (1 - \gamma)\, \mathrm{e}^{-\left(\frac{x}{\alpha}\right)^{\beta}},$$

Where p_c is percent correct of detecting the speed change, and x is speed-change extent (in percent of the base speed). Parameters α and β determine the threshold and maximum slope of the function, respectively [43]; γ is the performance expected at chance (0.5 in our case of a 2AFC). The *lapse rate* (upper asymptote) was constrained to be unequal to 0 and below 0.1, to avoid a biased estimate of the threshold [44]. The value of α, i.e., the stimulus intensity that is at the curve's point of inflection and predicts 81.6% correct performance, was defined as the detection threshold [43].

Goodness-of-fit for the psychometric functions was estimated using the function in the Palamedes toolbox, based on Wichmann and Hill [44]. The number of bootstrap simulations performed to determine the goodness-of-fit was 500. To test for influences of attention on performance, model comparisons were performed between the model based on the data of both conditions (valid and invalid cue) and the one treating the two conditions separately, using the Palamedes routine *PAL_PFLR_ModelComparison*. Transformed likelihood ratios of respective pairs of models were taken to be significantly different if exceeding 95% of transformed likelihood ratios obtained through Monte-Carlo simulations (10,000 simulations in each comparison). To quantify and further investigate attentional effects, subjects' speed-change detection thresholds were submitted to a three-way mixed-design ANOVA (Variables: *sign of speed change*, *stimulus eccentricity*, and *cue validity*). All standard statistical tests and descriptive statistics were performed with SPSS 18.0.

Results

Experiment 1

For each speed-change condition (acceleration and deceleration), a psychometric function was fitted to the detection rates of each subject, for 5° and 10° eccentricity, resulting in a total of 72 psychometric function fits (64 at the individual level and 8 at group level). Of these, 68 fits (94.4%) passed a goodness-of-fit test at the 5% level. Fig 2 shows the psychometric functions measured for one subject in our speed change detection task. Trials were collapsed across location (left and right) of the cue and target, and were classified as having a valid or an invalid cue (depending on whether or not the Gabor patches that changed speed indeed appeared at the

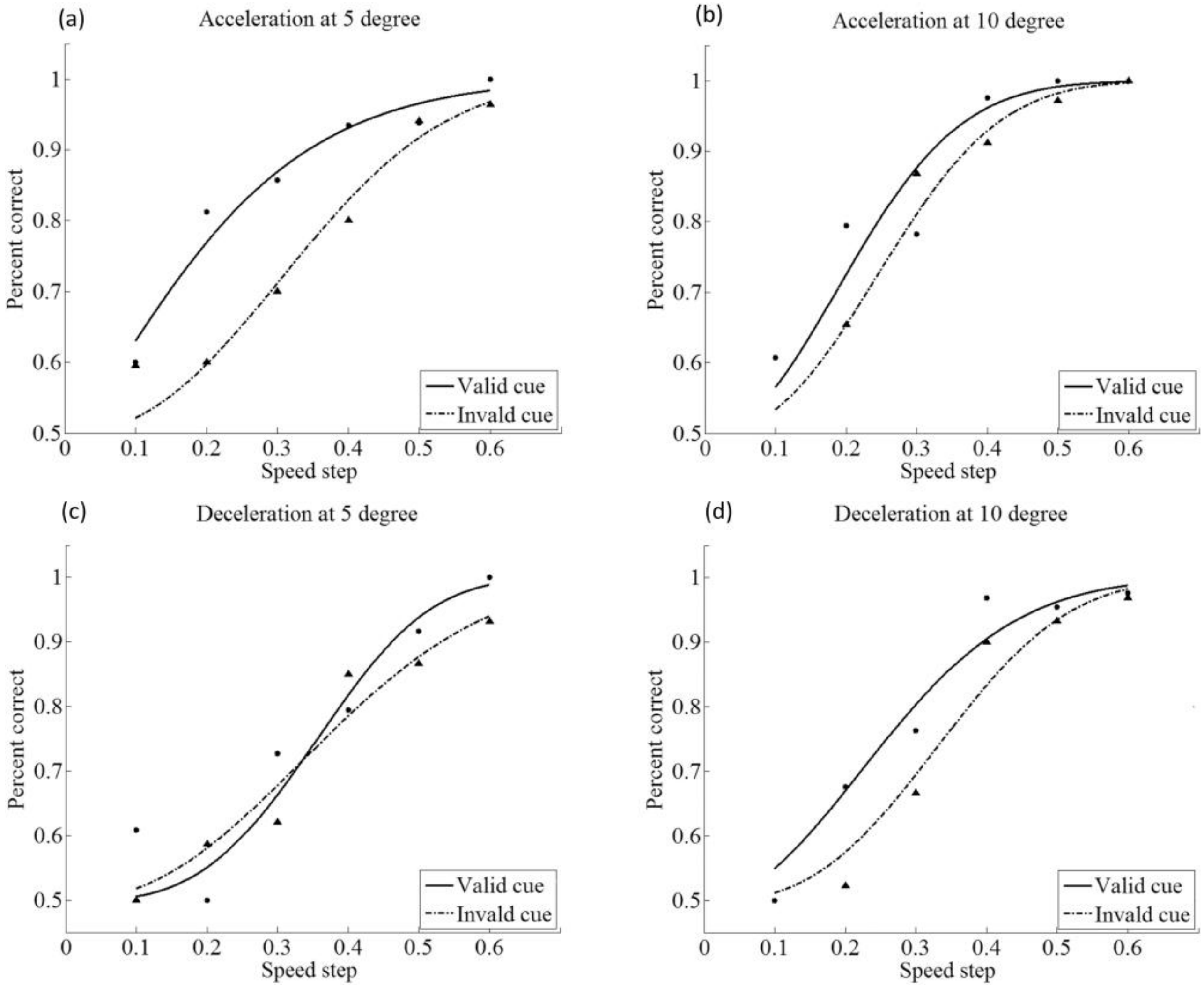

Fig 2. Effects of exogenous attention on performance (percent correctness) as a function of speed change step in Exp1. Solid lines are curve fittings for the valid-cue condition; dashed lines for invalid-cue condition. Acceleration is shown on top panels a and b, and deceleration in bottom panels c and d.

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cued location). When the target was cued, the valid-cue curve shifted to the left of the invalid-cue curve. Under the acceleration condition, the valid-cue and invalid-cue curves were significantly different from each other at both 5˚ and 10˚ eccentricity, as assessed by model comparison statistics (both $p < 0.05$). With deceleration, in contrast, the difference between valid-cue and invalid-cue curves did not reach significance at 5˚ ($p = 0.34$), whereas a significant difference was obtained at 10˚ eccentricity ($p < 0.05$).

Fig 3A and 3C plot the mean speed-change detection thresholds for the valid-cue and invalid-cue conditions at 5˚ and 10˚. The detection thresholds of the participants were analyzed using a 2×2×2 mixed ANOVA, with sign of speed change (acceleration or deceleration) as a between-subject factor, and cue validity (valid or invalid) and eccentricity (5˚ or 10˚) as within-subject factors. Overall, there was a rather large and significant main effect of cue validity, $F(1,14) = 17.538$, $p < 0.01$, $\eta_p^2 = 0.556$. Detection threshold for the attended target was much lower than for the unattended target, showing a facilitation effect of exogenous

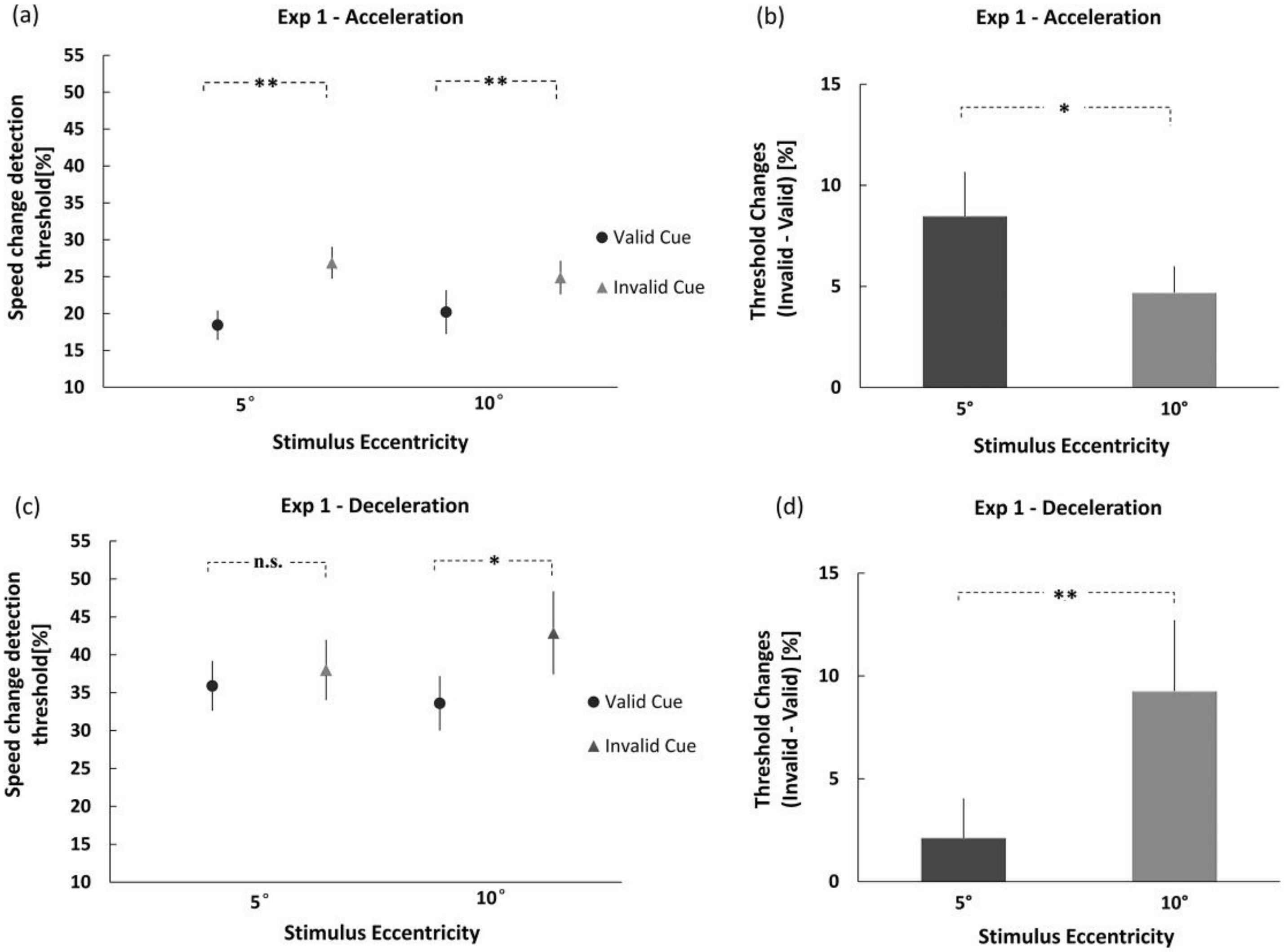

Fig 3. Effects of exogenous attention as indicated by speed-change thresholds in Exp 1. (a) The mean speed-change detection thresholds for acceleration in the valid-cue and invalid-cue conditions at 5° and 10°; (b) a larger exogenous cueing effect was observed at 5° under the acceleration condition; (c) the mean speed-change detection thresholds for deceleration in the valid-cue and invalid-cue conditions at 5° and 10°; (d) a larger exogenous cueing effect was obtained at 10° when the speed change was negative (* $p < .05$; ** $p < .01$; Error bars represent the standard error).

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attention. The main effect of sign of speed change was also large and significant, $F(1,14) = 14.691$, $p < 0.01$, $\eta_p^2 = 0.512$. The threshold to detect a deceleration was higher than that of acceleration (37.6% vs. 22.6%). Critically, a significant three-way interaction of sign of speed change, cue validity and eccentricity was observed, $F(1,14) = 13.710$, $p < 0.01$, $\eta_p^2 = 0.495$. To further explore the interaction, we performed 2×2 ANOVAs for acceleration and deceleration separately, with cue validity and eccentricity as independent variables. When the speed change was positive, the speed-change detection thresholds for the attended and unattended target, respectively, were 18.4% and 26.9% at 5° eccentricity, and 20.2% and 24.9% at 10°. In both pairs were the values significantly different (each p value < 0.01). Further paired t tests for the detection-threshold difference (unattended–attended) at 5° and 10° eccentricity indicated a larger exogenous cueing effect at 5° eccentricity than at 10° ($p < 0.05$; Fig 3B). In the deceleration condition, the difference between attended (35.9%)

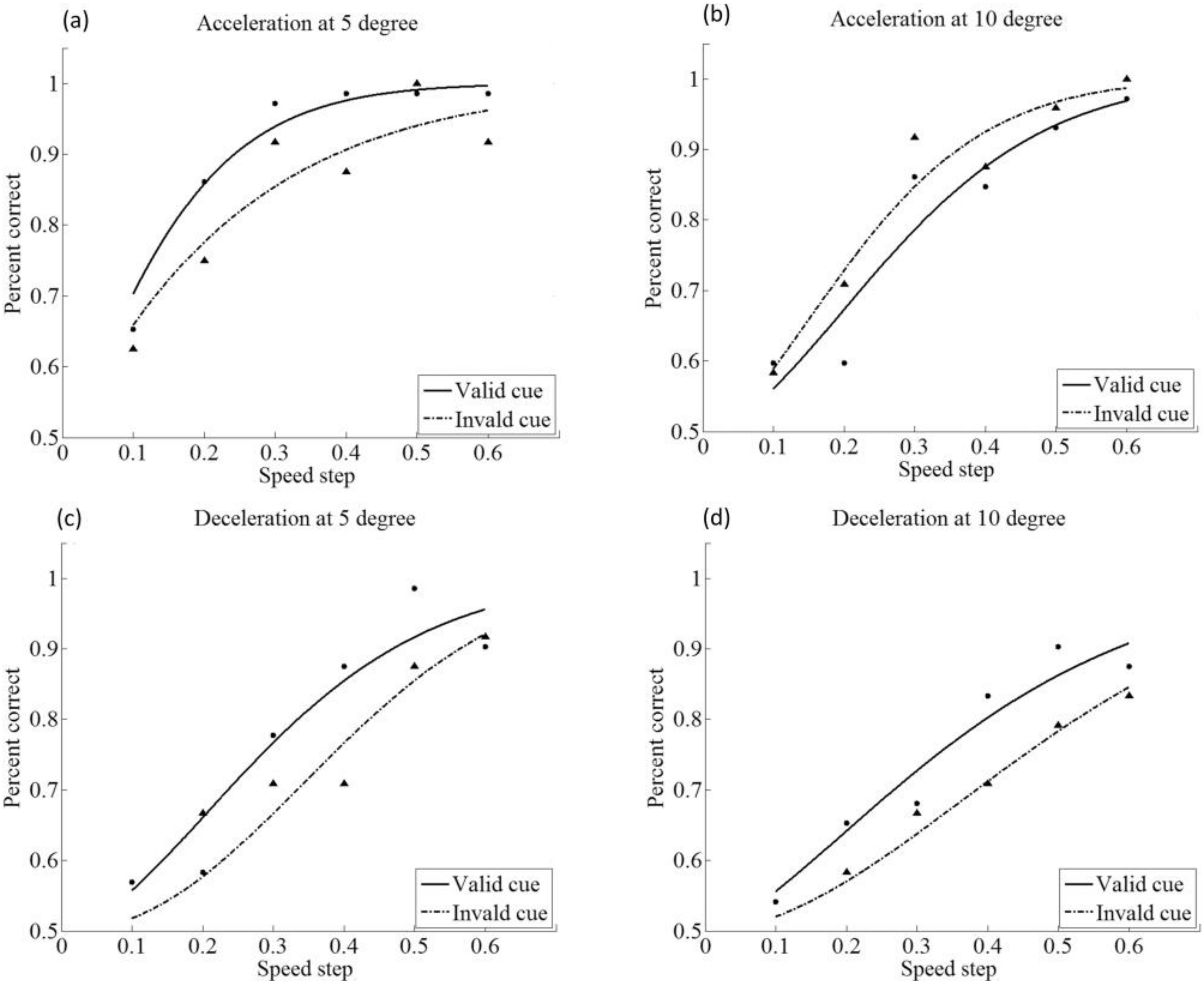

Fig 4. Effects of endogenous attention on the psychometric functions for speed-change detection in Exp 2. Solid lines are curve fittings for the valid-cue condition, dashed lines for the invalid-cue condition. Acceleration is shown on top panels a and b, and deceleration on bottom panels c and d.

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and unattended (38.0%) target was only 2.1% at the 5° condition, but was 9.3% at 10° eccentricity (33.6% vs. 42.9%). Only the latter difference was significant ($p < 0.05$). Further comparison of these two speed-detection threshold differences (unattended–attended) at 5° and 10° eccentricity showed that the difference under the 10° condition was significantly larger than that at 5° ($p < 0.01$; Fig 3D).

Experiment 2

Fitting the data to psychometric functions for the various conditions in Exp 2 followed the same procedures as in Exp 1. Among a total of 88 psychometric function fits obtained in Exp 2, there were 80 (i.e., 90.9%) that passed the goodness-of-fit test at the 5% level. Fig 4 shows the psychometric functions measured for one subject in the speed change detection task with endogenous cues. Significantly differing fits of valid-cue curves as opposed to invalid-cue curves by model comparison statistics were observed, both at 5° and 10° eccentricity (all $p < 0.05$).

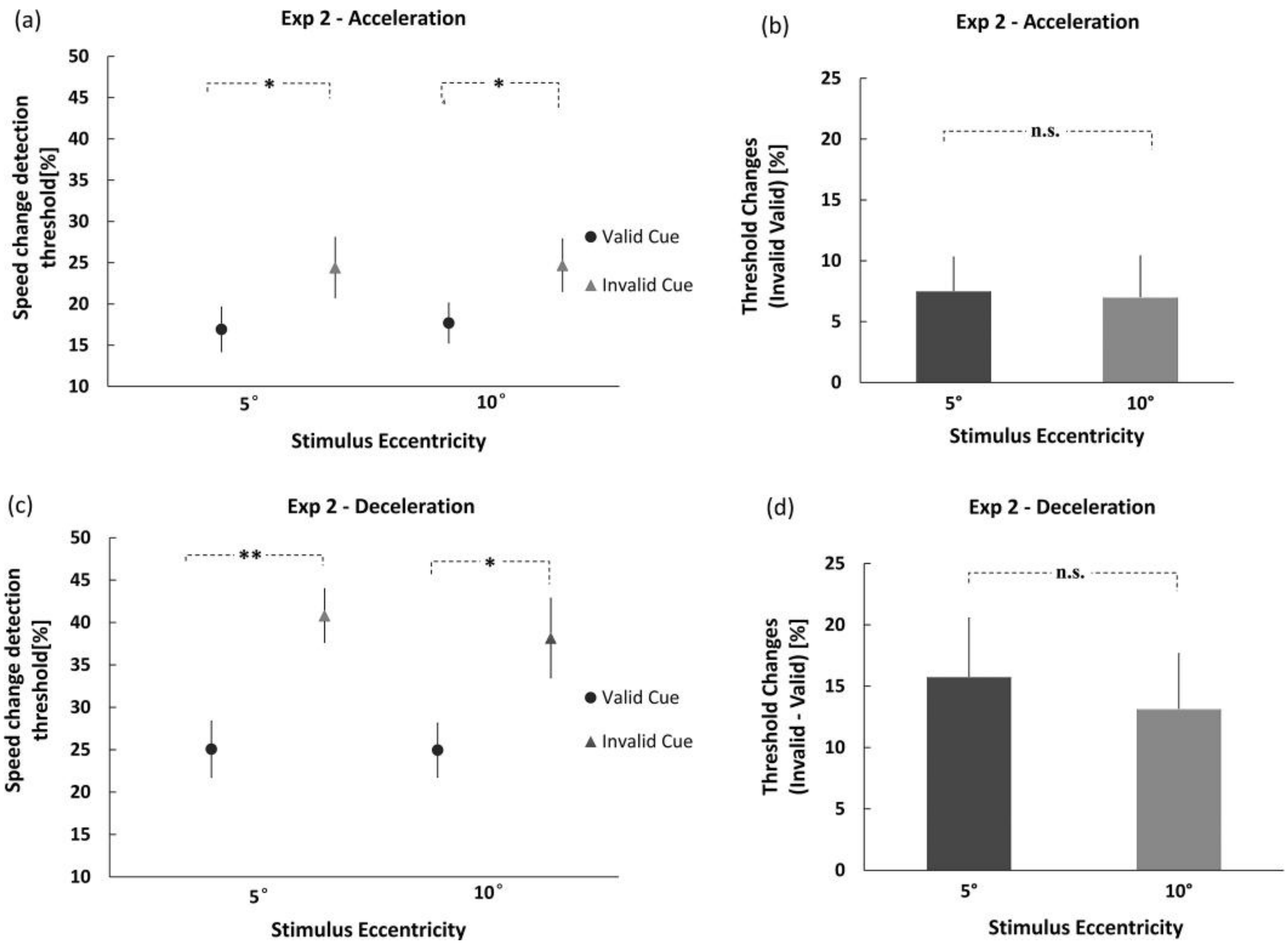

Fig 5. Effects of endogenous attention as indicated by speed-change thresholds in Exp 1. (a) Participants' speed-change thresholds for acceleration in different cueing conditions (valid and invalid), at 5° and 10° eccentricity; (b) roughly equal amounts of endogenous cueing effects were observed for acceleration at 5° and 10°; (c) speed-change detection threshold for deceleration in the valid and invalid cueing conditions, at 5° and 10° eccentricity; (d) there was no difference between the cueing effects for deceleration at 5° and 10° eccentricities (* $p < .05$; ** $p < .01$; Error bars represent the standard error).

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Participants' detection thresholds (Fig 5A and 5C) were submitted to a three-way ANOVA, with stimulus eccentricity (5° or 10°) and cue-target validity (valid or invalid) as within-subjects variables, and sign of speed change (acceleration or deceleration) as between-subjects variable. The ANOVA produced two significant main effects only: one for cue validity ($F(1,18) = 21.541$, $p < 0.001$, $\eta_p^2 = 0.545$), again showing the cue-induced decrease of threshold at attended compared to unattended locations, and the other for sign of speed change ($F(1,18) = 11.966$, $p < 0.01$, $\eta_p^2 = 0.399$). The detection threshold for deceleration was significantly higher than that of acceleration (32.2% vs. 20.9%). Since the sign of speed change is a between-subjects variable, we further conducted two separate 2×2 ANOVAs, with eccentricity and cue validity as variables, one for acceleration and one for deceleration. The results demonstrated that the there was no two-way interaction between cue validity and stimulus eccentricity, neither for acceleration nor deceleration ($ps > 0.05$). The lack of interaction indicates that the attentional modulation was independent of stimulus eccentricity. Nevertheless, the cueing effects were reliably observed in both acceleration and deceleration conditions: when the speed change was positive, the magnitudes of attentional effects (unattended–attended) were 7.5% for 5˚, and 7.0% for 10˚eccentricity; when the speed change was negative, the cueing effects were 15.7% for 5˚ and 13.1% for 10˚. No significant difference across eccentricity was obtained in either case (Fig 5B and 5D), which indicates endogenous cuing is not eccentricity-dependent.

Discussion

The results of the present study revealed that participants performed better in detecting and making decisions about the speed change when the target appeared in cued rather than uncued locations with the exception of exogenous attention for deceleration in the perifoveal region. A novel result of our study was that exogenous attentional modulation had differential effects at the perifoveal compared to the near-peripheral regions of the visual field, whereas endogenous attention enhanced performance to the same extent at the two eccentricities.

Our results are consistent with previous psychophysical studies demonstrating that spatial attention enhances sensitivity for basic visual dimensions at the attended location, such as contrast sensitivity, spatial resolution, reaction time, two-pulse resolution, and many others [1,2,3,4,5,45,46]. One might classify these dimensions into being of an either more static or more dynamic nature [5]; the present study would then provide another example of attentional modulation of perceiving dynamic stimulus information. Indeed, studies in monkeys and humans have demonstrated a correlation between MT-neuron activity and performance during detection of changes in motion attributes, suggesting that neurons in this brain area play a key role in this type of task [47,48]. A recent study further provided evidence showing that the population transients in area MT were tuned to represent the sign and magnitude of the corresponding speed changes [11]. Moreover, attentional modulation of performance in motion tasks and the motion-generated neural activity has been widely observed in psychophysical and physiological studies [6,49,50]. Taken together, thus, one possible explanation for our observed attentional effect on motion-change detection could be that responses of MT neurons to a sudden speed change occur earlier and are stronger when the change is attended to as compared to unattended, thus increasing the ability of neurons to signal those changes. Indeed, recently it has been shown that attention can enhance the amplitude of the motion-change-evoked response, and shorten response latencies, in area MT of the macaque monkey [51]. Another study also reported that the response of MT neurons to the motion-direction change occurred at a shorter latency when the change was attended to as compared to unattended [52]. Thus, attention can modulate such change-evoked neuronal activities and thereby influence behavioral change-detection performance. One alternative explanation for the lower detection threshold at attended relative to unattended locations is that attention decreases response variability and thus improves the signal-to-noise ratio of the change-induced response [53,54]. Furthermore, it could also be possible that the decisional or response bias towards reporting a change in the cued stimulus leads to a reduction of the threshold at these locations. In order to dissociate different factors from sensitivity change leading to the observed attentional cueing effect, future studies will be mandatory to expand the current findings and provide better understanding on the mechanisms underlying the attentional modulation on speed-change perception.

A central question in the current study was whether the attentional modulation is homogenous across eccentricities. Here we used the magnitude of speed-change detection threshold as index and found a novel differential effect of eccentricity for exogeneous attention modulation. For detecting acceleration, a larger exogenous cueing effect indexed by a lower threshold for the cued relative to the uncued conditions was observed in the perifoveal region (5˚) relative to the near-periphery (10˚). While for perceiving deceleration, the pattern was reversed. To be precise, a large exogenous cueing effect was demonstrated in the near-periphery (10˚), and no attentional modulation was observed in the perifoveal (5˚) visual field. Interestingly, a recent psychophysical study also observed a similar differential effect for speed change itself, namely a higher foveal sensitivity (lower threshold) for detecting acceleration and a higher peripheral sensitivity for deceleration [12]. Thus, we speculate that there are differences in the way exogenous cueing effects are propagated across the visual field when the speed change is positive vs. negative, and that attention has a larger modulatory effect at spatial locations that are more sensitive to speed changes. This link to sensitivity may reflect the importance of the goal of attention, which is to improve estimates of stimulus properties.

But, how can the observed eccentricity effect of exogenous attention modulation be understood within a general frame taking an ecological perspective also into account? We would like to submit a speculative hypothesis which is based on some previous observations. It has been shown that the visual field shows inhomogeneity with respect to sensitivity, i.e. a central cone of foveal and perifoveal vision which is surrounded by a plateau of relatively constant sensitivity in the peripheral visual field [30]; this structural inhomogeneity is observed also under scotopic adaptation [55] when the central cone of foveal and perifoveal vision becomes less sensitive compared to the plateau region. This structural inhomogeneity is also reflected in attentional control as has been demonstrated with the eccentricity effect of IOR which has been proven to be a stable phenomenon [35,39,40].

In spite of this inhomogeneity there are at least three mechanisms that guarantee homogeneity of visual processing, i.e. constancy of brightness throughout the visual field for suprathreshold targets under photopic adaptation conditions [55,56], a common time window of approximately three seconds when the time course of perifoveal and peripheral inhibitory effects of spatial attention is investigated [57], and on a more theoretical level the integration of sensory processing and motor control as it is hypothesized with the reafference principle [58]. As has been stated previously, within this theoretical account, different attentional fields represent service operations for an optimal processing of visuo-motor actions. Homogeneity of visual space is a necessary condition for an unbiased selection of potential visual targets; inhomogeneity of visual space reflects different mechanisms that are necessary for efficient action.

In the experiments on speed change perception reported here stimuli were presented at 5˚ or 10˚ eccentricities of the visual field. Based on the observations mentioned above it can be assumed that stimuli in these two stimulus positions are predominantly processed in two processing streams, i.e. one with the emphasis in the retino-geniculo-striate projection system (5˚ eccentricity), and one with the retino-colliculo-extrastriate projection system (10˚ eccentricity), although the latter is located in the border region of the two projection systems. However, as the experiments were done with a viewing distance of 57 cm (see methods), the visual axes of the two eyes had to converge by some degrees and also accommodation of the lenses were necessary which contribute in the near-distance space to size constancy [59]; these factors have been shown to modulate perifoveal sensitivity, i.e. modulating the transition zone between the central cone of foveal and perifoveal vision and the plateau region. Thus, we believe that in our experiments we are dealing with operational principles emphasizing the two anatomically different processing streams.

Embedded in the above general frame, how to understand the differential exogenous attention modulation in perifoveal and near-peripheral regions for detecting acceleration and deceleration respectively? Here we would like to further submit an ecological account with respect to attentional control in the visual space. As the perifoveal region and the periphery are typically involved in different cognitive functions, namely, object perception vs. spatial navigation, acceleration and deceleration of moving objects might trigger very different attentional processing modes. In the condition of acceleration, the speeded moving target might mimic an escaping prey being chased after. Therefore, a focused allocation of spatial attention is typically triggered, no matter where the target is. As attention can facilitate perception at the attended location, it is not surprising that we observed exogenous cueing effects at both perifoveal and peripheral locations. But why the cueing effect is larger at perifoveal relative to peripheral locations? This might be related to the different "attentional fields" in the visual field.

In research on the structural involvement of midbrain mechanisms in attentional control the size of attentional fields at different locations in the visual field could be inferred [60]. In those experiments the paradigm of central fatigue or habituation was employed when measuring light-difference thresholds at different locations in the visual field. It has been shown that continuous measurement of thresholds at one location results in habituation, i.e. the sensitivity decreases substantially and it takes ca. 20 minutes or so for spontaneous recovery. As habituation can be observed after monocular stimulation also in the non-stimulated eye, the habituation must be of central origin reflecting fatigue at the cortical level, and one is not dealing with retinal adaptation. The surprising effect reported by Singer and colleagues [60] is that habituation can be cancelled instantaneously if a mirror-symmetric position is stimulated. As spontaneous recovery takes a much longer time (20 minutes or so), an inter-hemispheric interaction has to be assumed. As the instantaneous resetting of threshold occurs also when an area is stimulated in a blind region (scotoma) of the visual field in patients who have suffered an injury in striate cortex, it can be concluded that the interaction between the two hemispheres takes place at the midbrain level [61]. In these experiments on resetting of thresholds it was possible to determine the spatial extent of the resetting area. It turned out that the retinal areas which contributed to such resetting were not limited to the exact retinal position possibly reflecting the diameter of receptive fields, but they were much larger and could be defined as "attentional fields". At 5° eccentricity the diameter of the attentional field is approximately 6° visual angle; at 40° eccentricity it is approximately 20° visual angle. Thus, a gradual increase of the size of attentional field from the perifoveal region to the periphery can be assumed. Although acceleration condition in the present study may trigger similar focused allocation of spatial attention to the cued location, the size of attentional field might be smaller for the 5° relative to the 10° eccentricity, thus leading to stronger attention power at the less eccentric location. As a consequence, a larger attention effect was observed for 5° relative to 10° eccentricity.

In the condition of deceleration, which perhaps signals potential danger such as a predator approaching us in a natural environment, we would like to propose that a divided attention mode is more likely to be triggered. However, divided attention to both visual fields is only possibly within a relatively small visual space such as within the perifoveal visual field and not beyond. This may explain why we did not observe any attention effect for the 5° eccentricity in the deceleration condition, since subjects' attention were equally distributed to both the cued and the uncued locations without any attentional bias. Since for 10° eccentricity the divided attention mode is presumably not possible and the subjects still have to activate the focused allocation of attention, the observation of an attention effect, i.e., a lower speed change threshold at the cued relative to the uncued location, is consistent with the activated attentional mode being triggered in such condition, as we speculate from an ecological perspective.

Note, however, that the sign of speed change was designed as a between-subjects factor, such that eccentricity effects observed in acceleration and deceleration conditions for the same stimulus eccentricity are not directly comparable. Future work using a full within-subject design will be particularly informative in disentangling this differential eccentricity effect of involuntary attention with respect to positive and negative speed changes.

Results from Exp 2 showed that endogenous attention also affects speed-change perception, but that, unlike in exogenous attention, the effects do not vary with eccentricity in the range measured. Directing endogenous attention via a foveal, informative cue to the target location improved speed change detection by the same amount at the two eccentric locations. This result suggests that top-down modulation is organized similarly in these regions. A recent study that manipulated either exogenous or endogenous attention in foveal and perifoveal locations (1° vs. 7°) has shown that exogenous attention had a larger cueing effect on reaction times for the perifovea than for the fovea, whereas endogenous attention improved performance at both eccentricities equally [62]. In a study by Yeshurun and colleagues [63] exogenous attention improved performance in a texture segmentation task at far eccentricities and impaired it at near eccentricities, whereas endogenous attention improved performance at all measured eccentricities. Together with the present findings, the most immediate inference appears to be that endogenous attention, being of top-down nature, can be consciously controlled and evenly distributed over the visual field, whereas exogenous attention relies on more hardwired, low-level mechanisms that operate differently in different regions of the central visual field. A next step will be to find out whether the observed dissociation between acceleration and deceleration for exogenous, but not for endogenous, attention holds up for other, more peripheral locations in the visual field.

In summary, while there is ample evidence for eccentricity-dependent modulation of spatial attention, the present study represents the first investigation of the attentional effects on speed-change perception in different locations in the visual field. The results suggest that exogenous attentional modulation has differential effects between the perifoveal and near-peripheral regions of the visual field, whereas endogenous modulation is homogeneous within the central 10°-radius field. Since these two types of attention have distinct effects on performance, they are most likely mediated by different mechanisms.

Supporting information

S1 Table. Percent correct for each subject under acceleration condition in Exp 1.
(XLSX)

S2 Table. Percent correct for each subject under deceleration condition in Exp 1.
(XLSX)

S3 Table. Thresholds for each subject in Exp 1.
(XLSX)

S4 Table. Percent correct for each subject under acceleration condition in Exp 2.
(XLSX)

S5 Table. Percent correct for each subject under deceleration condition in Exp 2.
(XLSX)

S6 Table. Thresholds for each subject in Exp 2.
(XLSX)

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Does cue processing modulate inhibition of return in a detection task?

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Abstract: While the abrupt onset of a peripheral visual cue usually leads to speeded responses to following targets at the cued relative to other positions, responses are slowed if targets lag behind the cue by more than ~200 ms. This response delay is termed *inhibition of return* (IOR) and has been considered as a mechanism to orient behavior toward novel areas. IOR has been found in both detection and discrimination tasks with later onset in discrimination tasks, probably due to a higher processing demand. Here we examined whether the processing demand of cues can modulate IOR in the detection task. The task to the peripheral cues, either color or gap cues, was passive viewing in one session (single task) and discrimination in another session (dual task). The results showed that the time course of IOR was resistant to the cue processing, while the magnitude of IOR was increased when the processing load became larger in the dual task relative to the single task. These results indicate that IOR in target detection is both reflexive in that its temporal dynamics remain invariant, and flexible in that its magnitude is modulated by task requirement.

Keywords: attention; cue processing; detection; discrimination; inhibition of return

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When a peripheral cue appears abruptly, responses to a following target at cued compared to uncued locations are facilitated when the stimulus onset asynchrony (SOA) between cue and target is short. However, an inhibitory effect can be observed if the SOA exceeds ~200 ms. This latter response delay has been termed as *inhibition of return* (IOR), which is assumed to reduce the probability of the reorienting behavior to previously visited spatial areas and objects, thus facilitating visual search to non-inspected targets (Klein, 1988, 2000; Ogawa, Takeda, & Yagi, 2002). Since its first report (Posner & Cohen, 1984), IOR has been consistently observed in detection and localization tasks (Bao & Pöppel, 2007; Bao et al., 2011, 2013; Bao, Zhou, & Fu, 2004; Fischer, Pratt, & Neggers, 2003; Hunt & Kingstone, 2003; Klein, 2000; Tanaka & Shimojo, 1996; Tassinari & Berlucchi, 1995; Zhou, 2008). With some exceptions (Tanaka & Shimojo, 1996; Terry, Valdes, & Neill, 1994), behavioral studies have also confirmed the presence of IOR in discrimination tasks, but often with delayed onset (Cheal, Chastain, & Lyon, 1998; Lupiáñez, Milán, Tornay, Madrid, & Tudela, 1997; Lupiáñez & Milliken, 1999; Lupiáñez, Milliken, Solano, Weaver, & Tipper, 2001; Pratt, 1995; Pratt & Abrams, 1999).

The different time courses of IOR in detection and discrimination tasks are explained by different task requirements on target processing (Klein, 2000; Klein, Castel, & Pratt, 2006; Lupiáñez & Milliken, 1999; Lupiáñez et al., 2001). It has been further shown that depth of cue processing can modulate the onset time of IOR in localization and discrimination tasks (Gabay, Chica, Charras, Funes, & Henik, 2012). However, there have been controversial evidences on the susceptibility of IOR to perceptual and cognitive influences from previous studies. On the one hand, IOR in detection tasks is resistant to modulations by temporal preparation (Milliken, Lupiáñez, Roberts, & Stevanovski, 2003) or cue predictability (Gabay & Henik, 2008); on the other hand, it is sensitive to cue-target similarity and cue-target overlap (Collie, Maruff, Yucel, Danckert, & Currie, 2000). Detection tasks, where only stimulus onset is processed, and discrimination tasks, which require detailed analysis of stimulus features, may employ different mechanisms (Srinivasan & Brown, 2006; Willis & Anderson, 1998). Therefore, it is interesting to ask whether the cue processing can also modulate IOR and its time course in detection tasks as it does in discrimination tasks (Gabay et al., 2012). Here, we addressed this issue by employing a detection task to targets while manipulating the cue processing demand by asking observers to either ignore or identify cue features. The relevant feature of peripheral cues was color in one session and orientation of a Landolt gap in another session. Our results showed a significant influence of cue processing demand on the magnitude of IOR but not on its time course, indicating that the development of IOR in target detection is relatively reflexive but its magnitude is subject to the task manipulation of cue processing.

Method

Participants

Twenty-four observers participated in the experiment (11 females; age range: 18–38 years, median age = 23.5 years), and all had normal or corrected-to-normal visual acuity and normal color vision. All participants gave written informed consent before the experiments and they received moderate rewards for their participation. The experiments had been approved by the Committee for Protecting Human and Animal Subjects in the School of Psychological and Cognitive Sciences at Peking University and were in accordance with the Declaration of Helsinki.

Stimuli and procedure

All stimuli were generated by a PC running MATLAB 7.0 with Psychophysics Toolbox extensions (Brainard, 1997) and were presented on a CRT monitor (Iiyama HM204DT, Vision-Master Pro514) with a refresh rate of 100 Hz. The background was set to black, and the fixation cross (0.2° × 0.2°) was set to gray (Figure 1A). Each trial began with an 800-ms display of a fixation cross and two gray placeholders (square rings with a size of 1° × 1°) followed by a 40-ms presentation of a peripheral cue. In the COLOR condition, the peripheral cue was a color change of one of the placeholders from gray to red or green, while in the GAP condition, one of the placeholders changed to a bright Landolt square ring with a 0.1° gap facing upward or downward. After the offset of the peripheral cue, there was an interval with variable durations (30, 60, 160, 310, 560, and 960 ms) in which only the fixation mark and the placeholders were presented, which was then followed by a yellow target disc (0.4° × 0.4°) presented within one of the placeholders until the observer responded. The target appeared with equal likelihood within the same (cued) or the opposite (uncued) placeholder as did the peripheral cue. Thus, the cue did not convey any information about where the target would appear. The placeholders were positioned symmetrically at 5° left and right of the fixation cross.

Each observer finished two task sessions successively. The first task was to detect the occurrence of the target by pressing a button using the left hand while ignoring the peripheral cue (SINGLE task). The second task was to both detect the target and discriminate the peripheral cue (DUAL task), where observers first made a quick response to the onset of the target using the left hand, and then judged the color in the COLOR condition or the gap position in the GAP condition of the peripheral cue by pressing one of two buttons using the right hand, in a manner counterbalanced across observers. In catch trials in each condition of each task, no target was presented and observers were instructed to withhold their responses, and the trial ended automatically after 1000 ms. A warning beep (1000 Hz) appeared for 100 ms whenever observers pressed the button before the target onset or during the catch trial. The inter-trial interval was randomly set to 1000–1400 ms.

Observers were seated in front of the screen with head on a chin rest and with a viewing distance of 57 cm. Each task session contained one block of COLOR cue and one block of GAP cue in an order counterbalanced across observers. Each block consisted of 192 target trials and 32 catch trials in random sequence. At the beginning of each block, observers performed 30–40 practice trials to

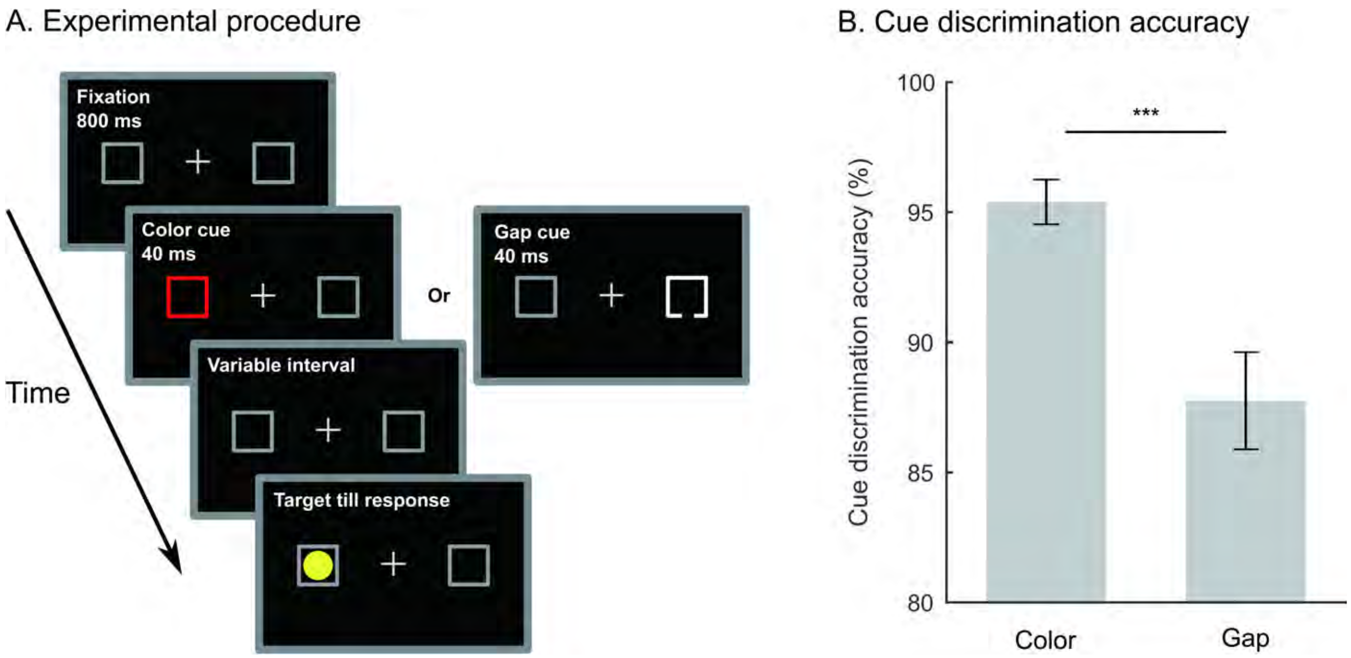

Figure 1. Illustration of the experimental procedure and performances of cue discrimination. (A) Following the display of a fixation cross and placeholders, a peripheral cue was presented (a red or green square ring in the COLOR condition and a Landolt square with a gap facing upward or downward in the GAP condition). After a variable interval, a yellow disc appeared in one of the placeholders until response. In SINGLE task, observers responded to the onset of the target; in DUAL task, observers first detected the target and then judged the color or the gap position of the cue. (B) Accuracy of cue discrimination in COLOR and GAP conditions in DUAL task. The performance was significantly better in the COLOR than in the GAP condition. ***$p < .005$.

get familiar with the task. Observers were instructed to fixate on the central cross during the task and take a short break after every 56 trials.

Results

Trials with response times (RTs) outside of 2 standard deviations of the mean or with physiologically impossible RTs (<120 ms) were excluded from further analysis. These trials accounted for 5.4% of the data. All observers successfully withheld their responses in catch trials of different tasks with different cue types (false alarm rate < 16%) except three males, whose data were thus excluded from further statistical analysis.[1] Accuracy of cue discrimination in the COLOR and GAP conditions in the DUAL task is shown in Figure 1B. Mean RTs were then calculated for each condition in each task, which are illustrated in Figure 2. The IOR effect (RT at cued location − RT at

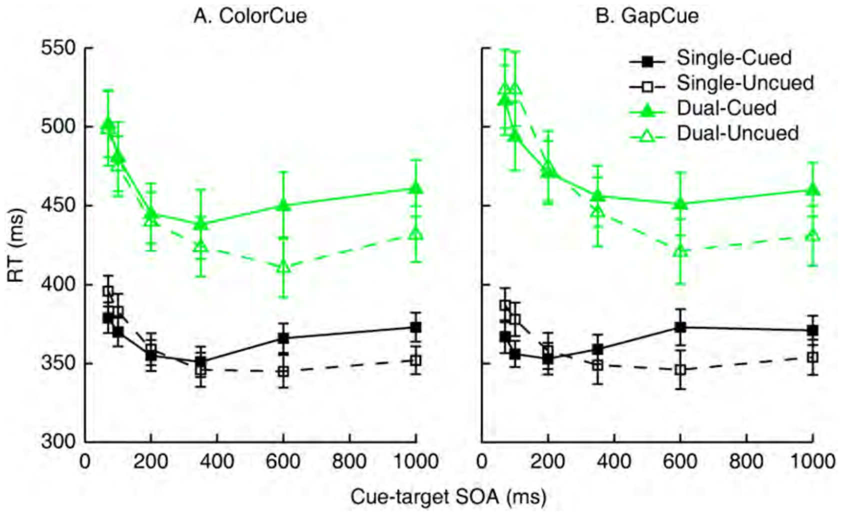

Figure 2. Mean response times (RTs) for cued (solid lines) and uncued (dashed lines) trials across stimulus onset asynchronies (SOAs) for different cue-processing conditions: (A) SINGLE (squares) and DUAL (triangles) tasks with COLOR cues; and (B) SINGLE (squares) and DUAL (triangles) tasks with GAP cues.

Table 1
Mean IOR ($RT_{cued} - RT_{uncued}$) Effect (ms) for Each Experimental Condition

	Single task		Dual task	
SOA (ms)	Color condition	Gap condition	Color condition	Gap condition
70	−18 (5)	−20 (4)	3 (5)	−6 (8)
100	−13 (6)	−22 (4)	6 (9)	−30 (8)
200	−4 (5)	−5 (4)	4 (8)	−3 (7)
350	4 (5)	10 (4)	15 (8)	10 (5)
600	21 (7)	26 (5)	39 (7)	30 (7)
1000	21 (5)	18 (5)	30 (8)	29 (9)

Note. Standard errors of means are depicted in parentheses. IOR = inhibition of return; RT = response time; SOA = stimulus onset asynchrony.

uncued location) for each experimental condition is shown in Table 1.

An analysis of variance (ANOVA) with factors of task (SINGLE and DUAL), cue type (COLOR and GAP), cue validity (cued and uncued), and SOA (70, 100, 200, 350, 600, and 1000 ms) was performed on the RT data.[2] There was a main effect of task, $F(1, 20) = 60.8$, $p < .001$, $\eta_p^2 = .75$, indicating faster responses in the SINGLE compared to DUAL tasks; a main effect of cue validity, $F(1, 20) = 9.9$, $p < .01$, $\eta_p^2 = .33$, revealing longer RTs for cued than uncued targets (IOR effect); and a main effect of SOA, $F(2.2, 44.0) = 52.0$, $p < .001$, $\eta_p^2 = .72$, showing a gradual decrease of RT with SOA. Consistent with previous findings of IOR (Klein, 2000; Tassinari & Berlucchi, 1995), cue validity interacted with SOA with an increased RT for cued relative to uncued targets at longer SOAs, $F(5, 100) = 33.3$, $p < .001$, $\eta_p^2 = .63$ (Figure 2). The change of RT along SOA was also affected by cue type and task, as indicated by interactions of Cue Type × SOA, $F(5, 100) = 3.3$, $p < .01$, $\eta_p^2 = .14$; Task × SOA, $F(2.2, 44.9) = 13.2$, $p < .001$, $\eta_p^2 = .40$; and Cue Type × Task × SOA, $F(5, 100) = 6.9$, $p < .001$, $\eta_p^2 = .26$. More interestingly, the interaction between task and cue-validity reached significance, $F(1, 20) = 7.6$, $p < .05$, $\eta_p^2 = .28$, showing that the increased RT to cued compared to uncued targets was larger in the DUAL relative to SINGLE task. There was also a triple interaction among cue type, cue validity, and SOA, $F(5, 100) = 2.7$, $p < .05$,$\eta_p^2 = .12$, suggesting that the cueing effect along SOA appeared different between COLOR and GAP cue conditions. To further clarify this triple interaction, we first pooled data from SINGLE and DUAL tasks and then calculated cueing effect by subtracting RT to cued targets from RT to uncued targets for different cue type and SOA conditions. Paired-samples *t* tests revealed significantly different cueing effects between COLOR and GAP conditions at short SOA of 100 ms, $t(20) = 4.1$, $p < .005$, but not at other SOAs ($ps > .2$), indicating that the cue type can modulate the facilitatory effect at short SOAs but not IOR at longer SOAs. These analyses suggest that cue processing can modulate the magnitude of IOR but has little influence on the onset time of IOR (around 200–350 ms, Figure 2).

We further examined the details of this modulation by dividing the data into three groups: short SOAs (70 and 100 ms), median SOAs (200 and 350 ms), and long SOAs (600 and 1000 ms). It is obvious in Figure 2 that the cueing effect for short SOAs is more facilitative, that for long SOAs is inhibitory, and that for median SOAs reflects the transition from facilitation to inhibition. Separate ANOVAs were then conducted on three SOA groups with factors of task, cue type, cue validity, and SOA. For short SOAs, Task × Cue Validity, $F(1, 20) = 4.4$, $p < .05$, $\eta_p^2 = .18$, Cue Type × Cue Validity, $F(1, 20) = 23.3$, $p < .001$, $\eta_p^2 = .54$, and Task × Cue Type × Cue Validity, $F(1, 20) = 4.4$, $p < .05$, $\eta_p^2 = .18$, reached significance, and post-hoc *t* tests revealed clear facilitation in the COLOR and GAP conditions with SINGLE task for both SOAs ($ps < .05$) and in the GAP condition with DUAL task for SOA of 100 ms ($p < .005$) but neither facilitation nor inhibition in the COLOR condition with DUAL task ($ps > .1$). For long SOAs, only task interacted with cue validity, $F(1, 20) = 5.0$, $p < .05$, $\eta_p^2 = .20$, indicating larger inhibitory effect (IOR) in the DUAL relative to the SINGLE task. Finally, for median SOAs, no significant interaction involving cue validity was found except the interaction of Cue Validity × SOA, $F(1, 20) = 11.7$, $p < .005$, $\eta_p^2 = .37$, which demonstrated the transition of cueing effect from facilitation to inhibition.

It is worth noting that the increase of processing demand from SINGLE task (passive viewing) to DUAL task (discrimination) is larger for Gap cues than for COLOR cues, which could be explained by the pre-attentive nature of color discrimination (Treisman, 1988; Treisman & Gelade, 1980) and the resource-dependent nature of gap judgment (Montagna, Pestilli, & Carrasco, 2009; Woodman & Luck, 1999). Our analysis of discrimination accuracies of peripheral cues also supported this discrepancy with respect to the processing demand in that lower performance values were obtained for GAP cues compared to COLOR cues

(Figure 1B). However, IOR magnitude was modulated by task (passive viewing vs. discrimination) instead of cue type (COLOR vs. GAP cues) in the current study, which might be explained by the processing-demand increase from COLOR discrimination to GAP judgment being not as strong as that from the SINGLE to DUAL tasks.

Discussion

By manipulating the task for the peripheral cues (passive viewing vs. discrimination) and their relevant features (color vs. gap position), the current study provided direct evidence for the relationship between the cueing effect and the cue processing demand. The results showed clear IOR in both the tasks with and without judgment of peripheral cues, as well as in both the conditions with color and gap cues, replicating previous findings (Gabay et al., 2012; Klein, 2000; Lupiáñez et al., 2001; Tassinari & Berlucchi, 1995). More interestingly, the processing level of cues (e.g., discrimination vs. passive viewing) modulated the magnitude of IOR but not its time course, contrary to predictions from previous observations (Gabay et al., 2012; Klein, 2000). Although a separate analysis revealed better discrimination performance for color cues than that for gap cues in the DUAL task, the difference of processing demands between judgments of color and gap position of cues was not as big as that between passive viewing and discrimination of cues to evoke significantly larger IOR in the GAP than in the COLOR conditions. Nevertheless, our results clearly demonstrate that the time course of IOR in target detection elicited by the abrupt onset of peripheral cues happens relatively reflexively and is difficult to be altered unlike the magnitude of IOR under situations with different cue processing levels. In the current study, with different tasks to cues and targets, the competition decreased and the RT cost would be alleviated or even reversed by attentional effect leading to facilitation (Figure 2). Also noticed in Figure 2 is the lack of facilitation at short SOAs for COLOR cue with DUAL task, which is probably due to confusion/cost by the color dimension of both cue (red or green) and target (yellow) with the task requirement of judging cue color. With a gap cue, there was less overlap between the features of cue and target and hence less cost, leading to manifest facilitation effect at short SOAs both in SINGLE and DUAL tasks.

Compared to detection tasks, IOR in discrimination tasks has been observed to be delayed (Cheal et al., 1998; Lupiáñez & Milliken, 1999; Lupiáñez et al., 1997, 2001; Pratt, 1995; Pratt & Abrams, 1999). Attentional dwell time (Klein, 2000), object integration window (Lupiáñez & Milliken, 1999; Lupiáñez et al., 2001), and the association between the locus coeruleus–norepinephrine system and selective attention (Gabay et al., 2012) have been attributed to the delayed onset of IOR in discrimination tasks, and suggest that the processing level of cues can modulate the time course of IOR (Gabay et al., 2012). However, we did not find similar modulation of the onset time of IOR by cue processing demand in the detection task, which was employed in the first demonstration of IOR (Posner & Cohen, 1984) and has been widely examined in more recent studies (Bao et al., 2011; Fischer et al., 2003; Hunt & Kingstone, 2003; Klein, 2000; Tassinari & Berlucchi, 1995). The lack of a cue processing effect on the time course of IOR in detection tasks likely reflects different attentional mechanisms involved in detecting and discriminating targets. As documented for decades, different aspects of a visual stimulus, such as luminance, form, and color, are processed by separate, parallel neural channels, from retina to higher visual cortical areas (Kaplan, 2004; Livingstone & Hubel, 1988). Such independent visual pathways could also activate different attentional mechanisms (Morrone, Denti, & Spinelli, 2002), modulating the neural activities in different regions of the cortex that are specialized for processing the selected features (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991). With respect to the signal processing, transient versus sustained attentional mechanisms have been conceptualized for some time (Jonides, 1981; Nakayama & Mackeben, 1989). Transient onset signals of stimuli are critical in target detection, whereas sustained signals encoding task-relevant features are important in target discrimination. This different emphasis of signal processing, homologous to the information processing along magnocellular and parvocellular pathways of the primate visual system (Kaplan, 2004), may also activate separate attentional orienting systems with different levels of reflexiveness. It is highly possible that target detection and target discrimination are modulated by attentional systems activated by transient and sustained signals, respectively, regardless of the task on cue being detection or discrimination. As a support for the dissociation of target detection and discrimination, IOR in detection tasks has been observed to be reflexive and not modulated by higher volitional processes, such as temporal preparation (Milliken et al., 2003) or cue predictability (Gabay & Henik, 2008). The absence of influence on the time course of IOR in the current study is also well in line with those observations, which are in contrast to the susceptibility of IOR in discrimination tasks influenced by temporal expectancy (Gabay & Henik, 2010) and cue processing level (Gabay et al., 2012). These findings together may reveal the distinct mechanisms responsible for IOR, at least for its time course, in detection and discrimination tasks, with the former being reflexive and the latter being subject to modulation. It will be an interesting topic to unveil the detailed neural pathways involved in IOR effect in detection and discrimination tasks in future studies.

The magnitude of IOR in the current study was indeed modulated by task requirement on peripheral cues, echoing previous findings that cue target similarity and cue target overlap could affect IOR in detection tasks (Collie et al., 2000). When a cue needs deeper processing, for example, in the task of discrimination compared to detection, more resources of spatial attention are allocated to the cue (Chen et al., 2008), which in turn increases the IOR effect when attention finally moves away from the cued position at long SOAs. In this regard, another dissociation of mechanisms underlying the IOR effect in detection tasks is hypothesized besides the separate IOR mechanisms for target detection and discrimination. One is for controlling the amount of attentional resources and is subject to the modulation by perceptual load or perceptual processing demand; the other is responsible for attentional allocation in time and is relatively reflexive. Although the dependence of IOR on cue target similarity and cue target overlap can also be explained by an altered IOR time course in detection tasks (Collie et al., 2000), our results confirmed the dissociated effects of cue processing on the magnitude and on the time course of IOR.

Taken together, the current study provides evidence that the task demand of a peripheral cue has little effect on the onset of IOR but can profoundly modulate the magnitude of IOR. We believe it is the first study in which the influence of cue processing on IOR in a detection task has been directly measured by manipulating the processing demand of the cue. The result has important theoretical implications and points to a dissociation of attentional mechanisms for target detection and discrimination as well as a disentanglement of mechanisms controlling attentional resources and attentional allocation in time.

Declaration of conflict of interest

The authors declare that there are no conflicts of interest.

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Notes

[1] When data from these three males were included in the analysis, similar results were obtained.

[2] Greenhouse–Geisser correction of degree of freedom was reported whenever the sphericity assumption was violated.

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SHORT COMMUNICATION

Sadness and happiness are amplified in solitary listening to music

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Abstract Previous studies have shown that music is a powerful means to convey affective states, but it remains unclear whether and how social context shape the intensity and quality of emotions perceived in music. Using a within-subject design, we studied this question in two experimental settings, i.e. when subjects were alone versus in company of others without direct social interaction or feedback. Non-vocal musical excerpts of the emotional qualities happiness or sadness were rated on arousal and valence dimensions. We found evidence for an amplification of perceived emotion in the solitary listening condition, i.e. happy music was rated as happier and more arousing when nobody else was around and, in an analogous manner, sad music was perceived as sadder. This difference might be explained by a shift of attention in the presence of others. The observed interaction of perceived emotion and social context did not differ for stimuli of different cultural origin.

Keywords Emotion · Music perception · Social context · Attention · Sadness · Happiness

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Introduction

Music has often been referred to as the "language of emotion", and some empirical studies have reported that listeners make similar ratings of musically expressed emotions, thus suggesting that music conveys emotional meaning (Gabrielsson and Juslin 1996; Juslin and Sloboda 2010; Park et al. 2014, 2015). Basic emotions like happiness or sadness in a piece of music are conveyed by means of acoustic and musical features (Gabrielsson and Lindström 2010) such as pitch level (e.g. a higher pitch for expressing joy), tempo (e.g. a slower tempo being related to sadness), or tone (e.g. ascending tones for a more pleasing experience). These observations suggest that emotional meaning of music is partly based on anthropological universals, which are shared across cultures and presumably controlled by common temporal mechanisms (Bao et al. 2015; Pöppel 1989).

Many studies using categorical or scalar measurements emphasize a distinction between one's perception of musical emotion and the emotion evoked by music (Gabrielsson 2002; Scherer and Coutinho 2013). Perceived emotion is the emotion recognized in the music, thus corresponding to an external locus (Evans and Schubert 2008), whereas induced emotion (also known as felt emotion) is the emotion experienced by the listener, thus corresponding to an internal locus. Although perceived and felt emotions coincide in most cases (Evans and Schubert 2008; Schubert 2013), they may differ in certain circumstances. In this regard, listeners may sometimes experience more positive or even pleasant than negative emotions when listening to sad-sounding music (e.g. nostalgia, tenderness, wonder, peacefulness, and transcendence; see Garrido 2017; Kawakami et al. 2014; Taruffi and Koelsch 2014; Sachs et al. 2015; Schubert 2016). Perceived emotions refer to a rather objective apperception, while felt emotions are more relevant to the subjective nature of personal experience with music (Park et al. 2013). We chose to investigate perceived emotions in music rather than felt emotions for two reasons. The first is that perceived emotions are less influenced than felt emotions by short-term factors (Sloboda 1991); the second is that responses of perceived emotion are more consistent than responses of felt emotion (Eerola and Vuoskoski 2013; Gabrielsson and Juslin 1996).

Perceived musical emotion is not entirely encapsulated within a musical structure. The experience of music, like aesthetic experiences in general, is based on a complementarity of “bottom-up” sensory information processing and “top-down” mechanisms, which are shaped and modulated by memory (Silveira et al. 2012), expectations (Silveira et al. 2014, 2015), and situational factors like the social context. Most of the time, people are exposed to music in the company of others. Being surrounded by others is common during various activities of every day’s life, e.g. at work, at a store, and in public transportation. The presence of others not necessarily involves social interaction and connection. With regard to music listening, there are different types of group settings, e.g. the presence of others while listening together with direct interaction, the presence of others while listening together without direct interaction (e.g. music in public), and the presence of others without listening together and without direct interaction (e.g. music on headphones in public). The present study was designed to mimic situations of the second case; these situations are characterized by an engagement in similar activities without direct or explicit interaction.

While some experiments in social psychology provide theoretical perspectives and empirical evidence to explain how people affect and influence one another in various domains (e.g. Allport 1985; Cialdini and Goldstein 2004; Echterhoff et al. 2009; Zajonc 1965), group-level phenomena of an individual’s perception of musical emotion are still unclear. Previous research has only been conducted on felt musical emotions, showing that the experience of music does differ when it is heard privately versus in a group setting, in particular with regard to valence (Juslin et al. 2008, Taruffi and Koelsch 2014), arousal (Egermann et al. 2011), and intensity (Gabrielsson and Wik 2003; Liljeström et al. 2013). Also social context has been found to take influence on arousal and valence dimensions of induced emotions. Social feedback, i.e. positive or negative evaluations of the music by others, led to upward or downward manipulation of appraisals (Egermann et al. 2009). Given that perception and evocation of emotion are interconnected processes, social context may also affect perceived emotion. Thus, the current study aims at a deeper understanding of whether and how social context affects the perception of musically expressed emotions.

Emotions can be defined in a two-dimensional space by the independent axes valence, i.e. happy–sad continuum, and arousal, i.e. excited–relaxed continuum (Russell 1980; Russell and Barrett 1999). In the past two decades, about one-third of music and emotion studies have used a dimensional model (Eerola and Vuoskoski 2013). While the discrete emotional space has shown to be too limited to fully capture the complexity of emotional reactions to music (Larsen and Stastny 2011), the validity of the two-dimensional representation of emotions in music has been confirmed in many studies (Juslin and Sloboda 2001; Zentner et al. 2008). We therefore used a self-report measure of valence and arousal while listeners heard musical excerpts that represent one of two emotions, respectively (happiness and sadness). Deploying a valence dimension, we aimed at investigating whether the perceived quality of musical emotion is modulated in a social context. We tested two alternative hypotheses. In case subjects rate happy music happier and sad music less sad in one of the conditions, i.e. valence-ratings are generally more positive, this result would suggest that listening to music in a particular social context shifts people’s perceptions of musically expressed emotions to more pleasantness. However, if participants report that happy music sounds happier and sad music sadder in a certain condition, i.e. ratings are closer to the poles on the valence dimension, this result would indicate that this setting amplifies perceived emotions in music.

Music perception is not only embedded in a proximal social context, but also in the context of culture. There is evidence for cultural variations in music perception, in particular with regard to pleasantness ratings for consonant and dissonant note constellations (McDermott et al. 2016). Besides, particularly prevalence as well as appreciation of sad music is not given in all cultures. It has previously been found in cross-cultural studies that some basic emotions in music appear to be universally perceived in music from a different culture, including joy and sadness (Balkwill and Thompson 1999; Balkwill et al. 2004; Fritz et al. 2009). These comparisons use a discrete model of emotion in music, yet a within-subject comparison of perceived emotion in music from ones own or a different culture using a dimensional model of affect has not yet been studied. Thus, we selected musical stimuli from two different cultures, i.e. Western and Eastern, to explore associations or dissociations in the perception of emotions expressed by music from one’s own or a different culture. This will give further insights into anthropological universals and cultural specifics (Bao and Pöppel 2012) underlying perception of emotions in music.

Methods

Participants

Sixteen Chinese students (7 males, mean age = 24.1 years, SD = 3.4 years, age range = 18–31 years) of Peking University, Beijing, China, participated in the experiment after giving written informed consent. All participants had normal or corrected-to-normal visual acuity, were right-handed, and reported to have normal hearing. In order to minimize the confounding effect from musical education (Bigand et al. 2005), we defined previous formal musical training or art expertise as exclusion criteria. To keep differences between subjects to a minimum, we also defined the preference for a specific music genre as an exclusion criterion.

Materials and Apparatus

Eighty musical excerpts of 30 s each (40 traditional Chinese music pieces and 40 Western classical music pieces) served as experimental stimuli. All excerpts were taken from non-vocal music, and music genres were kept consistent. This choice was based on previous research, which suggested that musical emotions may differ across genres due to their inherent musical differences (Kreutz et al. 2007). Besides, lyrics may add some semantic meaning for perceived emotion in music. The focus on classical music serves the purpose of comparability as this is the genre predominantly used in previous studies. All musical excerpts were selected by the authors in consultation with an expert musicologist. They were tested in a pre-study on a 9-point Likert scale regarding valence (from 1 = sad to 9 = happy), arousal (from 1 = calm to 9 = excited), familiarity (from 1 = unfamiliar to 9 = familiar), and aesthetic appeal (from 1 = not aesthetically pleasing to 9 = aesthetically pleasing). Fifteen subjects (6 males, mean age = 22.7 years, SD = 2.0 years, age range = 19–26 years) participated in the pre-study. Stimuli were selected based on mean ratings of valence and were categorized into two emotional qualities: happiness ($M = 6.40$, $SD = 0.68$) and sadness ($M = 4.08$, $SD = 0.71$). Selection criterion for stimuli was a mean rating within a confidence interval (95%) established for the particular type of emotion. We avoided selecting well-known pieces as well as pieces of high social preference to eliminate the possible confound from personal memory (see Table 1 for a list of selected musical excerpts' mean ratings and standard deviations associated with those means).

The musical stimuli were played on a PC (DELL Vostro420) and presented via Harman-Kardon multimedia speakers at a comfortable volume level that was kept constant between all participants.

Procedure

All participants listened to the 80 music excerpts in a solitary and a group setting. Thus, the study was conducted in two testing sessions at different days. Condition order was randomized and counterbalanced across participants, i.e. half of the participants came in for the solitary session first and the other half for the group session. Also the presentation order of the musical excerpts was randomized for both the solitary and the group listening conditions for each participant.

In the solitary listening condition, participants sat 1.4 m in front of a pair of loudspeakers. During the presentation of stimuli, participants were instructed to listen carefully to the music. After each excerpt, participants assigned ratings on a 9-point Likert scale for valence from one (completely sad) to nine (completely happy), and for arousal from one (completely calm) to nine (completely excited). The increment of the scale was 0.5. Participants were asked "How would you describe the emotional content of the music itself?". They were given instructions to make an assessment of the emotions expressed by the music, rather than the emotion felt by themselves, i.e. "How HAPPY/SAD did the music SOUND?", rather than "How HAPPY/SAD did the music make YOU feel?". There was no time limitation for evaluating the stimuli. In the group listening condition, participants were seated in a semicircle facing forward. This allowed each of them to be quite aware of the other's presence without enabling them to communicate with each other (i.e. visually, verbally, or by seeing the other's ratings). This setting was chosen to prevent direct social interaction and feedback that is known to influence music perception (Egermann et al. 2009). The procedure was kept constant with the solitary condition, except of a fixed inter-stimulus interval of 40 s. Participants also made

Table 1 Means and standard deviations for stimuli selected based on pretest ratings for each music type and cultural style

Cultural style	Music type	Valence value	Arousal value	Aesthetic value	Familiar value
Eastern	Happy	6.43 (0.69)	6.06 (0.61)	6.14 (0.76)	4.97 (0.93)
	Sad	4.05 (0.57)	3.87 (0.63)	6.22 (0.77)	4.99 (0.78)
Western	Happy	6.38 (0.68)	6.13 (0.74)	6.54 (0.61)	4.51 (0.51)
	Sad	4.12 (0.86)	5.02 (0.96)	6.21 (1.06)	4.35 (0.67)

the same set of interpersonal ratings as in solitary listening condition.

Data analysis

We conducted a 2 × 2 × 2 repeated measures ANOVA with the three independent variables: music type (happy vs. sad), social context (solitary vs. group), and cultural style (Chinese vs. Western). The dependent variables of interest were ratings of arousal and valance given by participants after the presentation of each music excerpt. The descriptive data analysis and ANOVA were performed using SPSS for Windows (version 21.0).

Results

The three-way ANOVA on valence-ratings revealed a significant main effect for music type, $F(1,15) = 74.99$, $p < .001$, $\eta_p^2 = 0.83$, and a significant interaction between music type and social context, $F(1,15) = 9.32$, $p < .001$, $\eta_p^2 = 0.38$. Further analyses using Bonferroni procedure indicate that mean scores on the valence dimension were higher during the solitary condition ($M = 6.14$, $SE = 0.143$) compared to the group condition ($M = 5.63$, $SE = 0.195$, $p = 0.019$) for happy musical excerpts. For sad music, a significantly lower mean score was observed for solitary listening ($M = 3.99$, $SE = 0.148$) relative to group listening ($M = 4.32$, $SE = 0.181$, $p = 0.025$) (see Fig. 1a). There was also a significant interaction between music type and cultural style, $F(1,15) = 9.32$, $p < .001$, $\eta_p^2 = 0.305$. Participants tended to give higher scores to Chinese happy music ($M = 6.01$, $SE = 0.168$) compared to Western happy music ($M = 5.76$, $SE = 0.141$, $p = 0.070$), and lower scores to Chinese sad music ($M = 3.99$, $SE = 0.187$) compared to Western sad music ($M = 4.32$, $SE = 0.154$, $p = 0.063$); however, those contrasts only reached marginal significance levels (Fig. 1b).

The mean arousal-ratings were analysed using a 2 × 2×2 repeated measures ANOVA. Critically, we observed a significant interaction between music type and social context, $F(1,15) = 5.65$, $p = 0.031$, $\eta_p^2 = 0.27$. Further analyses to decompose this significant two-way interaction displayed that the arousal-ratings for happy music were significantly higher during the solitary condition ($M = 6.30$, $SE = 0.119$) as compared to the group setting ($M = 5.90$, $SE = 0.161$, $p = 0.007$) (Fig. 2a). There was no significant difference between solitary and group listening for sad music (M(solitary) $= 4.76$, SE(solitary) $= 0.165$; M(group) $= 4.90$, SE(group) $= 0.182$, $p = 0.161$). There was a significant main effect for music type, $F(1,15) = 25.66$, $p < .001$, $\eta_p^2 = 0.63$, and cultural style, $F(1,15) = 47.64$, $p < .001$, $\eta_p^2 = 0.76$. These two factors significantly interacted with each other, $F(1,15) = 69.50$, $p < .001$, $\eta_p^2 = 0.82$. Further analysis

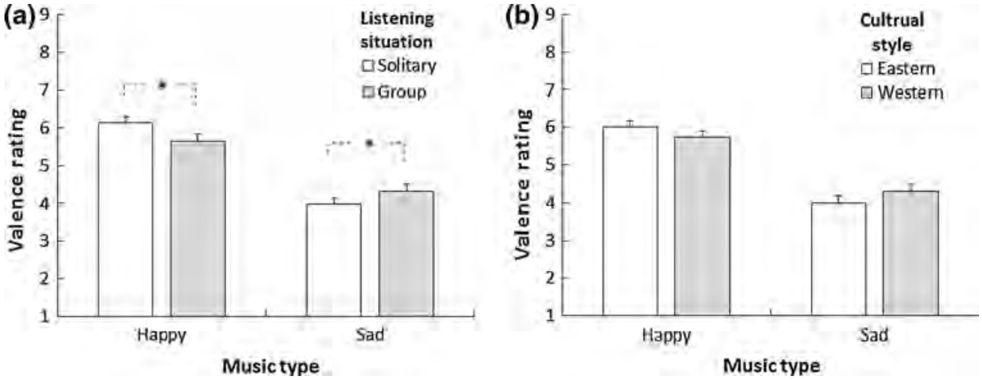

Fig. 1 **a** Mean valence-ratings for happy and sad music across listening situations (solitary vs. group); **b** Mean valence-ratings for happy and sad music from different cultural styles (Eastern vs. Western). *Note.* Asterisks indicate significant effects: *<.05

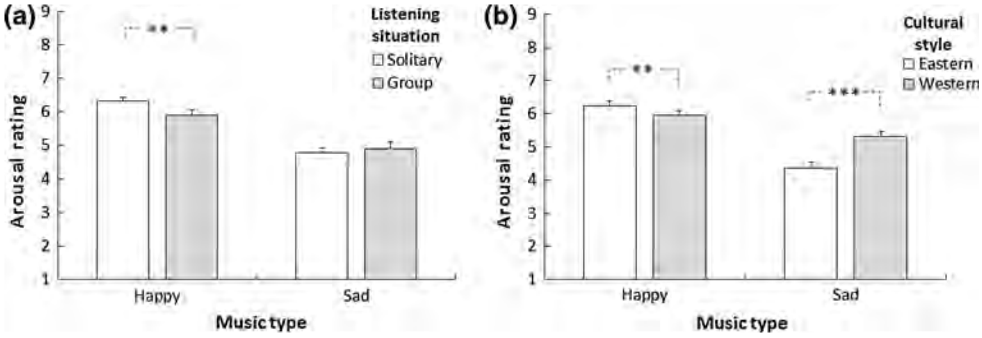

Fig. 2 **a** Mean arousal-ratings for happy and sad music across listening situations (solitary vs. group); **b** Mean arousal-ratings for happy and sad music from different cultural styles (Eastern vs. Western). *Note.* Asterisks indicate significant effects: **<.01; ***<.001

showed that the ratings of perceived arousal were higher in Chinese music ($M = 6.24$, $SE = 0.142$) compared to Western music ($M = 5.85$, $SE = 0.124$) for happy musical excerpts ($p = 0.006$). When participants listened to the sad music, perceived arousal was lower in Chinese music ($M = 4.36$, $SE = 0.175$) relative to Western music ($M = 5.29$, $SE = 0.149$, $p < .001$) (see Fig. 2b).

Discussion

In the current study, we investigated the effect of social context on the perception of musically expressed emotions. Our results support the notion that social settings as defined by the mere presence of others alter the perceived emotion, which is conveyed by music. More specifically, in terms of valence, happy music was rated less joyful and less arousing when experienced in a group setting. For sad music, listeners perceived musical excerpts as less sad in the presence of others. While limited in generalizability with regard to music genres, cultural samples, and type of group setting, the results suggest that perception of both musical valence and arousal is subject to social influences.

Participants converged on a polarized pattern towards happy for happy music and towards sad for sad music during the solitary listening condition. The observations support the hypothesis that listening to music privately amplifies perceived emotional valence and do not support the alternative hypothesis that solitary listening shifts those perceptions positively in that happy pieces of music are experienced as more happy and sad pieces as less sad. The design of our study suggests that these changes in perceived emotion are not based upon social feedback, i.e. not the valence that others attribute to the musical piece modulates the subject's appraisal of emotional valence. This provides a new perspective on social effects when evaluating musically expressed emotions, indicating that the mere presence of others might generally diminish the quality of perceived musical emotion.

With regard to arousal, our results show that the emotion perceived in happy music was rated as more arousing when heard alone. For sad music, no significant differences were found between the two conditions for the arousal-ratings. This indicates that arousal levels perceived in music, i.e. how exciting or relaxing a piece of music is perceived, are more stable for sad than happy music. Eventually, certain musical characteristics of sad music, e.g. tempo or loudness, are related to this phenomenon; however, this interpretation remains speculative and needs further testing.

One possible explanation for the present results is that solitary and group settings facilitate different modes of attention. It might be assumed that self-focused attention has a larger scope to operate on evaluations of musical emotions in a solitary listening condition. Complementarily, in a group setting, attention is additionally focused on the presence of others. Therefore, being alone might give the listener a better opportunity to turn focus inwards, given that there is no division of attentional resources between processing the thoughts and feelings of oneself and others. In line with this, solitude could provide a suitable environment for reflecting on musical emotion. Previously, self-focused attention has been used to explain modulations of felt musical emotions (Scheier and Carver 1977, Ziv 2004) within a culturally imprinted frame (Chentsova-dutton and Tsai 2010). Given that attention and perception are bidirectionally interconnected in bottom-up and top-down processes as represented in brain activations (Vuilleumier 2005), we assume that a shift of attention might be underlying modulations of perceived musical emotion. In this regard, it is possible that the group setting diminishes attention not only to the self, but also to the music. The mode of attention when alone allows us to enter more deeply into the idiosyncratic world when exploring perceived emotions, leading to amplified ratings of musically expressed emotions with happy music appearing more happy and sad music appearing more sad. Future research is needed to clarify whether the relation of affective perception and attentional focus explains the modulation of rating scores by social context.

It is worth noting that the participants did not receive any explicit social feedback from group members in our experimental setting. Thus, they did not know about the ratings given by other study participants, i.e. any form of social feedback that might influence the evaluation of stimuli, nor were they encouraged to think and feel about one another, which may increase the feeling of togetherness and render the experienced stimulus more intense (Egermann et al. 2009; Salganik et al. 2006). The relatively little information regarding the others may make it less likely that direct social appraisal took place. We expect that social influence on the perception of musical emotions in a natural group music listening setting (such as a live concert) is far stronger than in our study, because visual input is more direct and explicit, e.g. by rhythmic body movements. Yet, our findings nevertheless suggest that a social context defined as the presence of others listening to the same music without direct interaction exerts an effect on the emotions perceived in music. This might be understood with regard to the notion of embodied cognition (see for an overview Wilson 2002), i.e. the way the body is situated in a certain situation exerts effects on cognition, perception, and emotion. This highlights the role of the body, not only in affective responses towards a musical piece, but also in decoding the emotional content of it. A methodological shortcoming of the experimental manipulation is the lack of time limitation in the solitary listening condition, which might have led to differential decision-making processes. Yet, we consider a time window of 40 s in the group condition long enough to potentially enable reasoning, changes, and adjustments in ratings.

A significant interaction between music type (happy or sad) and cultural style (Western or Eastern) was only observed for the arousal dimension. With participants of our study being born and raised in an Eastern culture, this indicates that listeners' arousal-ratings displayed a polarized pattern corresponding to their own dominant cultural background. Perceived arousal was higher for happy music and lower for sad music of the own compared to a different culture. While for sad music this effect might be confounded by the selected stimulus material (see Table 1), at least for happy music this effect might be indicative of cultural imprinting. The classification of emotions in joyful or sad was found to marginally differ for musical pieces of different cultures: perception of positive and negative affective qualities in music was amplified for pieces of one's own culture. While both familiarity and preference of the specific musical excerpts were controlled in our experiment, it might be that these interactions are related to familiarity with music of one's own culture in general. Interestingly, however, there was neither a two-way interaction between cultural style of the musical excerpts and our experimental manipulation (solitary or group listening) nor a three-way interaction between cultural style, music type, and experimental manipulation. Thus, the effect of social context on perceived emotions in music is similar for musical excerpts from different cultures.

Given that communication of emotional expression in music may transcend cultural boundaries (Balkwill and Thompson 1999; Fritz et al. 2009), it is reasonable to argue that the categorization of basic emotions (such as happy or sad) applies in a similar manner to musical expressions from different cultures. This indicates an understanding of emotions communicated by acoustic and musical features, which is universal, but it still leaves room for differences in perceived emotional intensity. In our study, cultural context is represented in the stimulus material, and not in variations of cultural group settings. Due to cultural differences in social behaviour, our results cannot be generalized to other cultural groups. Future cross-cultural investigations will be mandatory to expand these preliminary findings and further test anthropological universals as well as cultural specifics in musical emotion perception.

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ORIGINAL RESEARCH
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Aesthetic Preferences for Eastern and Western Traditional Visual Art: Identity Matters

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Western and Chinese artists have different traditions in representing the world in their paintings. While Western artists start since the Renaissance to represent the world with a central perspective and focus on salient objects in a scene, Chinese artists concentrate on context information in their paintings, mainly before the mid-19th century. We investigated whether the different typical representations influence the aesthetic preference for traditional Chinese and Western paintings in the different cultural groups. Traditional Chinese and Western paintings were presented randomly for an aesthetic evaluation to Chinese and Western participants. Both Chinese and Western paintings included two categories: landscapes and people in different scenes. Results showed a significant interaction between the source of the painting and the cultural group. For Chinese and Western paintings, a reversed pattern of aesthetic preference was observed: while Chinese participants gave higher aesthetic scores to traditional Chinese paintings than to Western paintings, Western participants tended to give higher aesthetic scores to traditional Western paintings than to Chinese paintings. We interpret this observation as indicator that personal identity is supported and enriched within cultural belongingness. Another important finding was that landscapes were more preferable than people in a scene across different cultural groups indicating a universal principle of preferences for landscapes. Thus, our results suggest that, on the one hand, the way that artists represent the world in their paintings influences the way that culturally embedded viewers perceive and appreciate paintings, but on the other hand, independent of the cultural background, anthropological universals are disclosed by the preference of landscapes.

Keywords: beauty, culture, aesthetics, visual perception, Chinese painting, Western painting

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INTRODUCTION

The concept of beauty is a complex topic since antiquity, and this is especially true when tracing the cultural trajectory of our relationship with beauty. Western and Eastern artists tend for instance to use different perspectives to represent the visual world, both in the geometric and in a metaphorical sense. Viewers from different cultures and social groups may have distinct aesthetic experiences to the same visual displays (Palmer et al., 2013). Cultural differences might explain why beauty is attributed to some things, but not to others (Jacobsen, 2010). Aesthetic processing can only be understood, if it is also seen as being embedded in cultural contexts and being modulated by social conditions.

Unlike Western painters who since the Renaissance tried to create an exact view of a visual environment, Chinese painters never developed a notion of space as a measurable geometrical entity by developing mathematical rules to organize space and create precise spatial relations (Delahaye, 1993). Instead, the Chinese outlook emphasizes a dynamic structure for human relations with the environment, even with the universe, independent of exact physical representations or the proper imitation of objects (Sullivan, 1984; Cameron, 1993). Pictorial perspectives employed in Western and Chinese paintings are, thus, fundamentally different. Western painters tried to create an exact view of what they see (or what they believe to see); the geometric perspective was developed to create the illusion of three-dimensionality by means of a single-point or convergent perspective (Kubovy, 1986). It should, however, be pointed out that the central perspective in Western art is already an abstraction (Worringer, 1908), and it is not at all a geometrically correct representation of what we see. Mechanisms of size constancy (Pöppel, 1988) recalibrate the projection of visual stimuli on the retina at the cortical level, and thus distort what is mathematically defined. This neural operation in the early visual pathway (Zhou et al., 2016) serves the purpose to maintain the identity of the perceived object. Thus, the different trajectories of abstraction in the Eastern and Western cultural environments have created unique conceptual frames.

Chinese painters have employed specific ways of emphasizing spatial information compared to Western painters. Besides a typical arrangement of spatial information in a vertical manner (i.e., far objects appear in the upper part while close objects appear in the lower part of a scroll painting), a most common means of suggesting distance was perhaps the use of a perspective, where parallel diagonal lines strike off from the plane of the picture. The distinctive characteristics of parallel projections is that lines parallel in fact are also parallel in the drawing. The angles of these obliques are coherent throughout the plane (Tyler and Chen, 2011). Moreover, Western artists are inclined to capture a specific moment in a visual scene and fix the physical position of the viewer. In contrast, when looking at a Chinese landscape painting, there is no distinct point to guide viewers. The Chinese outlook has a dynamic quality that integrates successive time windows (Bao et al., 2015), and encompasses a panoramic view of the visual scene, which can be perhaps associated with a floating view (Tyler and Chen, 2011).

Another concept with respect to differences between Eastern and Western landscapes (Pöppel, 2006) distinguishes on the psychological level between an internal view ("Ich-Nähe" in German) and an external view ("Ich-Ferne" in German); (it should be mentioned in passing that in this area of research many publications are available in other languages that remain mute for the only English-speaking scientific community). The central perspective in Western art (with its misunderstood geometrical law) represents an external point of view, and it is characterized by its own aesthetic values; the visual world is expanding in front of the eyes of the viewer (Ich-Ferne). Other than implied by Masuda et al. (2008) who refer to this view as "insider perspective," we characterize this external view as "Ich-Ferne." In Eastern landscapes a completely different psychological mechanism is initiated when viewing a picture from a floating perspective. Because of the multi-layer viewpoints on top of each other on a scroll form, the spectator has the impression being invited to shift one's position dynamically, sometimes being located in the air (e.g., looking downward from above), sometimes being located on the ground (e.g., looking at scenes straight ahead), and sometimes being located at a lower land (e.g., looking upward at faraway mountains); much more importantly, however, is the psychological consequence of this shifting position that the viewer becomes subjectively a part of the scene. The multi-layer perspectives can be considered to simulate a three-dimensional space resulting in a virtual circle or ellipse vertical to the picture; within this imaginary circle or ellipse the viewer becomes part of the scene depicted in front of the eyes. This implicit construction of subjective space creates the feeling of belongingness or "Ich-Nähe." Thus, we want to submit that the floating perspective does not represent an "outsider perspective" (Masuda et al., 2008).

Another interesting difference with respect to perspective in a more general sense is related to the pictorial subjects of Western and Chinese paintings. Western artists favor object-centered scenes, whereas Chinese artists prefer context-oriented scenes. Paintings in the West typically seek to make the object salient, i.e., to distinguish the object from the background (Masuda et al., 2008). In China it has been otherwise; Chinese artists put great emphasis on the context, often with a meditative theme showing small human figures, as if humans are embedded in a natural environment and awed or inspired by a mountainous landscape (Turner, 2009), or even overwhelmed by the sublime (Burke, 1757).

Previous research on culture and aesthetics has demonstrated indeed substantial cultural variations in artistic expressions, such as in drawings, photography, city design, product design, or else (for a review, see Masuda et al., 2012). By analyzing the ratio of the horizon drawn to the frame and the number of objects used in 15th to 19th century paintings from East Asian and Western countries, Masuda et al. (2008) provided evidence showing that the East Asian artists placed horizon lines higher than Western artists, and that the size of models in East Asian masterpieces was smaller than that in Western ones. Furthermore, this cultural variation in artistic expressions persisted in landscape drawings of contemporary adult members of North American and East Asian cultures. This pioneer study and subsequent research (Wang et al., 2012; Ishii et al., 2014; Nand et al., 2014; Senzaki et al., 2014) have shown that cultural variations in artistic expressions are empirically testable and robust from a methodological point of view.

However, with respect to this methodological point, another critical factor has to be considered when comparing artifacts from different cultures. According to the theory of mutual constitution between culture and the mind (Shweder, 1991; Morling and Lamoreaux, 2008), people should prefer artistic expressions which reflect their own cultural systems. This prediction is based on the idea that people who are exposed to different types of cultural artworks could internalize their preference for them. To date, several studies have documented cultural influences on a wide range of psychological processes, notably attention, motivation, reasoning and self-concept (Markus and Kitayama, 1991; Nisbett et al., 2001; Han and Northoff, 2009).

In spite of the vast knowledge already gathered (e.g., Masuda et al., 2008; Ishii et al., 2014; Senzaki et al., 2014), we believe that it is still useful to look at one more detail when comparing Eastern and Western art, and possibly evaluating the results within a different frame of reference. Thus, the present study addresses one central question: Are different representations as expressed in typical traditional Chinese and Western paintings appreciated differently by people from different cultural groups? To answer this question, we explored the possibility of cultural differences in aesthetic preferences of contemporary members from the two cultural groups: Chinese and Westerners. We hypothesized that Western and Chinese subjects would show distinct aesthetic preferences due to the implicit application of cultural patterns of artistic expression from their own cultures. This hypothesis on "cultural imprinting" is in line with previous observations (Bao et al., 2013b, 2014) in which it was shown that the language environment shapes temporal processing when a tonal and a non-tonal language are compared; this process is suspected to take place on an implicit level by informal learning (Pöppel and Bao, 2011). It is furthermore suggested that the analytic and holistic strategies are employed also in cognitive processes when representatives from the Eastern and Western cultures evaluate visual artwork validating previous work (e.g., Masuda et al., 2008).

MATERIALS AND METHODS

Participants

Forty-six university students (23 Chinese and 23 international students from Western countries) participated in the experiment. The Western students were from US, Canada and Europe with 15 males and 8 females. They were aged from 18 to 31 years old with an averaged age of 23.74 years. None of the Western participants had lived in China for more than 4 years. The Chinese subjects consisted of 9 males and 14 females, aged from 19 to 30 years old with an averaged age of 23.35 years. All participants had normal or corrected-to-normal visual acuity and color vision, were right-handed, and had no history of neurological disease. None of them were specialists in art history or art theory. Participants were asked before the experiment about their preference on painting style. They generally did not show any specific interest in a certain painting style. All subjects were given informed written consent before the experiment. The study was approved by the departmental ethical committee of Peking University.

Apparatus

The experiment was conducted in a dimly illuminated room to reduce visual distraction. Picture presentation was controlled by the E-prime software system (Schneider et al., 2002a,b) and displayed on a 19-in CRT monitor (1024*768 resolution, 100 Hz refresh rate). Responses were collected through a keyboard.

Materials

Sixty traditional Chinese paintings and 60 Western classicist paintings were selected from the archives of http://www.artcyclopedia.com and http://www.namoc.org by the authors in consultation with an art specialist. Both Chinese and Western paintings included two categories, namely, landscapes, and people in a scene. The category "landscapes" refers to depictions that treat nature as the primary topic, and mainly includes sky, mountains, rivers, trees, flowers, meadows, houses, and boats. The category "people in a scene" depicts more than one person engaged in activities, coexisting with backgrounds of the land, thus distinguishing it from portraits. The paintings were chosen from a variety of historical periods (from the 9th to the 18th century). We trust to have selected an appropriate sample of pictures, but we are aware of the fact that some hidden bias may have remained uncontrolled; one has to acknowledge that it is impossible to draw in a statistical sense a "true" random sample from artwork, because the population from which to draw the sample is not definable due to the cultural and historical complexity. In spite of these constraints we believe to have chosen a fair sample of typical pictures from the two cultural environments. To come closer to the goal of an appropriate comparison, all paintings were low in emotional intensity, that is, they did not depict sexual, aggressive, or religious themes. All paintings were prepared in uncompressed bitmap file format, and the image dimensions varied. Graphic manipulation of stimuli was done using Photoshop (Adobe). Each combination of cultural style (Chinese vs. Western Painting) × pictorial subject (landscape vs. people in a scene) includes 30 images. Another 40 images (with 10 images in each condition) were selected from the same database (from which the images for the main experiment were selected) and used in the practice session before the main experiment.

Procedure

All paintings were presented in random order. Each picture was presented once during the experiment. After viewing each picture subjects were asked to judge its beauty on an 8-Point Scale by pressing one of eight buttons on a keyboard, where 1 indicated very ugly and 8 indicated very beautiful. We also recorded reaction time (RT), but stimulus presentation was self-paced and participants were instructed to approach the paintings in a subjective and engaged manner. Before the main experimental trials, subjects were given 10 practice trials under each condition so they could establish a general impression of the stimuli to be presented. The images used in the practice trials were not used in the experiment.

RESULTS

The beauty-rating data were subjected to a three-way mixed analysis of variance (ANOVA) with Cultural Style (Chinese vs.

Western Painting) and Pictorial Subject (landscape vs. people in a scene) as two within-subjects variables and Participant Group (Chinese vs. Westerner) as one between-subjects variable. The ANOVA revealed a significant interaction between Participant Group and Cultural Style $\{[F(1,44) = 9.247, p < 0.01, \eta_p^2 = 0.174]\}$, while both main effects of Participant Group and Cultural Style were not significant $\{[F(1,44) = 2.597, p = 0.114, \eta_p^2 = 0.056]$ and $[F(1,44) = 0.010, p = 0.919, \eta_p^2 = 0.000]$ respectively$\}$. Further analysis of this interaction displayed interesting beauty-rating patterns between the two participant groups: for the Chinese group, a significantly higher score was observed for Chinese paintings relative to Western paintings (5.18 vs. 4.72, $p < 0.05$). For the Westerner group, a reversed pattern was observed, i.e., a significantly higher score was demonstrated for Western painting as compared to Chinese painting (4.78 vs. 4.36, $p < 0.05$) (**Figure 1**). This double dissociation result pattern suggests that Chinese and Western participants prefer paintings that correspond to the background within which they were culturally imprinted.

The ANOVA produced only one significant main effect for the Pictorial Subject $[F(1,44) = 37.478, p < 0.001, \eta_p^2 = 0.502]$; this factor interacted with Cultural Style $[F(1,44) = 19.338, p < 0.001, \eta_p^2 = 0.305]$. For both Chinese and Western paintings, participants gave higher scores to landscape than to the category "people in a scene" (**Figure 2**). Further analysis revealed that the difference in scores between Western landscape and figure paintings was significantly larger than that for the Chinese ones (1.20 vs. 0.60, $p < 0.001$) (**Figure 3**). No other main effects or two-way interaction reached significant level. The three-way interaction was also not significant $[F(1,44) = 0.549, p = 0.463, \eta_p^2 = 0.012]$.

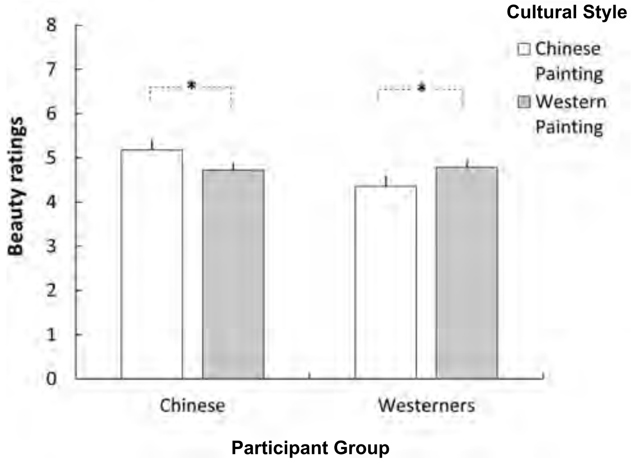

FIGURE 1 | The significant interaction between Cultural Style (Chinese vs. Western Painting) and Participant Group (Chinese vs. Westerners) on beauty rating. Chinese and Western participants showed preferences for their own culture's paintings: Chinese participants gave higher aesthetic scores to traditional Chinese paintings than Western paintings, whereas Western participants did the opposite. $^*p < 0.05$.

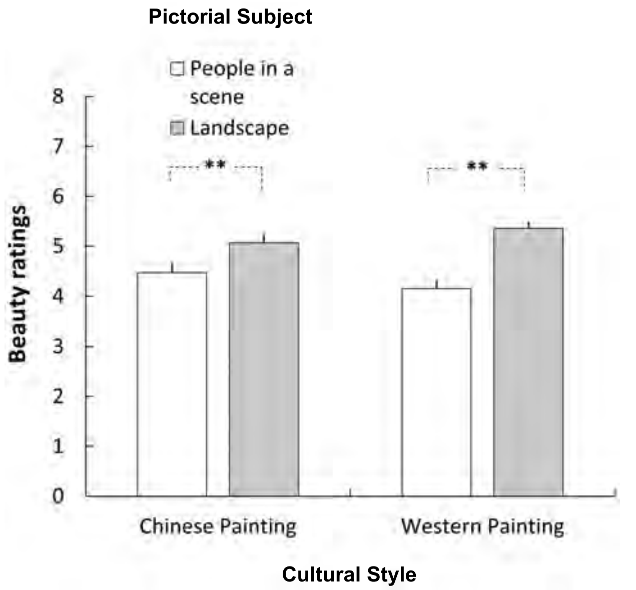

FIGURE 2 | Beauty rating of paintings as a function of Cultural Style (Chinese vs. Western Painting) and Pictorial Subject (landscape vs. people in a scene). Both Chinese and Western participants gave higher aesthetic scores to landscape than the people in a scene. $^{**}p < 0.01$.

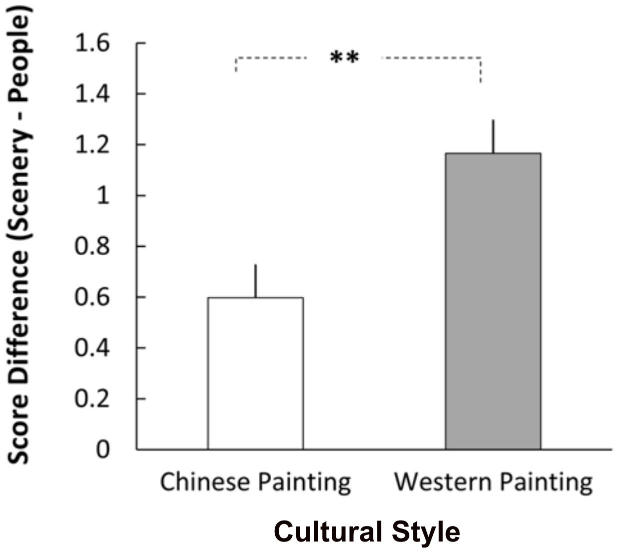

FIGURE 3 | The difference in aesthetic scores (landscape – people in a scene) was significantly larger for Western paintings than that of Chinese paintings. $^{**}p < 0.01$.

DISCUSSION

Research in the past has shown that by using stimuli from the arts, i.e., from music, poetry or visual arts, one can obtain new insight into cognitive mechanisms which may remain undetected if one focuses only on simple stimulus configurations as have been employed in the tradition of classical psychophysics (e.g., from our own research environment: Silveira et al., 2012; Avram et al., 2013; Lutz et al., 2013; Pöppel et al., 2013; Zaytseva et al., 2014; Park et al., 2015). With the study reported here, we want to further contribute to this research paradigm by comparing the appreciation of art in subjects from the East and the West with its challenging differences (Pöppel and Bao, 2016). The present study investigated aesthetic preferences of two cultural groups using pictorial representations from the different cultures as stimuli. Our results showed that subjects prefer paintings that correspond to their own cultural traditions, i.e., each cultural group evaluated the paintings from their own culture as more beautiful.

This result at first sight might not at all be surprising as it might simply reflect the well-known "in-group bias" or "in-group favoritism" effect (e.g., Tajfel et al., 1971). One could argue that the subjects immediately recognize whether they are confronted with a picture from the East or from the West, and Eastern subjects feel more familiar with pictures from their cultural background whereas the contrary is true for the Western subjects. If the in-group bias applies in this case, one has to add, however, further arguments, which explain the direction of the bias, because such a bias cannot be anticipated with respect to "aesthetic evaluation." In the case that Eastern subjects would have evaluated Western pictures as more beautiful, and Western subjects would have preferred Eastern pictures (which also could have happened), one would also deal with in-group bias, but with a reversed direction. Thus, it is necessary to find a reason for the direction of the observed bias in our study. With respect to this question we want to return to one hypothesis outlined above that Eastern and Western pictures create a different psychological state of involvement or "belongingness“ (Ich-Nähe vs. Ich-Ferne). It is argued that the pictures trigger a culturally specific feeling of identity (Pöppel, 2010). A Western subject looking at a Western picture is supported in his feeling of cultural identity, and the same is true for an Eastern subject when looking at an Eastern picture. We want to submit that the creation and maintenance of identity is one of the most fundamental challenges of the human mind (Zhou et al., 2014), and artwork of one's own cultures may serve as an important psychological mechanism.

Our analysis may be supported by a recent study in which it was reported that when viewing traditional Chinese landscape paintings, Chinese subjects experienced a greater level of relaxation and mind-wandering, and a lower level of object-oriented absorption than when viewing Western realistic landscape paintings (Wang et al., 2014). With respect to cultural identity, the study by Masuda et al. (2008) may also support our viewpoint; they reported that East Asian subjects were more likely to include great details and background when drawing a scene or taking photographs of a model compared to Western subjects.

Some further points have to be appreciated: It has been argued that Westerners apply more rational or logical methods to a wide range of intellectual and artistic pursuits, in which a mathematical orientation plays an important role (Kline, 1964). Western paintings, hence, emphasize the creation of realistic scenes as much as possible. In contrast, Chinese artists place more faith on intuitive and aesthetic knowledge about nature (Golas, 2014). This faith is bolstered by considerable reliance on personal feelings and emotions embedded into the image, rather than the details and exact appearance provided by sensory modalities. Members of different cultural groups are repeatedly exposed to various examples of visual images from their respective cultures, and they may implicitly gain knowledge (Pöppel and Bao, 2011) about the dominant aesthetic representation of the world; thus, the appreciation of paintings that obey aesthetic principles within their culture is facilitated.

Consistent with Shweder's (1991) argument that psychological processes and cultural products represent two sides of the same coin, Morling and Lamoreaux (2008) further suggested that culture and the mind are mutually constructed. A given cultural meaning system is internalized by members of the culture, and those who internalize that system display habitual ways of thinking and acting. A recent study by Ishii et al. (2014) showed that European Americans preferred unique colorings and Japanese preferred harmonious colorings, and these preferences were positively associated with cultural values, i.e., uniqueness among European Americans and harmony among Japanese participants. Another study (Wang et al., 2012) found that East Asians were more likely than their European Canadian counterparts to prefer the moderately complex webpage to the simple portal page, and the results could be explained by the fact that the Western way of thinking is more self-contained and independent, while most East Asians are more holistic and context oriented. These previous findings, combined with the present results, provide supportive evidence that people indeed prefer artistic expressions which reflect dominant cultural meaning systems.

A surprising result in our study is that both Western and Chinese subjects prefer landscapes compared to the category "people in a scene." This observation suggests that in spite of the cultural frame of aesthetic appreciation as noted above there may exist an overriding principle with respect to the sense of beauty reflecting an anthropological universal (Bao and Pöppel, 2012). Such an overriding principle at a lower perceptual level is for instance observed in color preferences. Komar and Melamid systematically examined the artistic preferences of people in ten countries, and found that the most preferred painting was an idealized blue landscape (Wypijewski, 1997). There is indeed evidence that color preferences are universal across cultures (e.g., Eysenck, 1941), although later research revealed that both similarities and differences may exist (Taylor et al., 2013). A strong case, however, for a universal color preference has been made for blue (Saito, 1996; Ou et al., 2004).

From the viewpoint of Darwinian aesthetics (or "evolutionary aesthetics"), it has been suggested that humans may be biologically primed to find particular features more beautiful, because these features may have been selected for optimal survival, for instance allowing better decisions about when to move, and where to settle, and what activities to engage in (Thomhill, 1998; Zaidel, 2010). However, evolutionary theorists have been criticized for regarding art only with respect to adaptive preferences (Plotkin, 2004). Apart from ultimate adaptive valence, we are given no criteria by evolutionary aesthetics theories for explaining why some objects are generally perceived as aesthetically superior. Here we suggest that the present finding that landscape is aesthetically more appreciated is not only because it signals restfulness or safety, but also because its restful or safe features carry added emotional significance.

It is worth noting that the difference between the preferences of landscape and people in a scene was higher for Western paintings compared to Chinese paintings. The aesthetic basis of Chinese paintings is deeply affected by the philosophy of Chinese Taoist ideas that emphasize the harmonious relationship between human beings and the cosmos (Law, 2011). In the eyes of Chinese artists, natural scenes have the power to suggest the very essence of life to human beings, and in unobtrusive ways, may therefore act as inspirations to virtue. Indeed, in Chinese landscape paintings we can find tiny human figures, such as a fisherman on a lonely boat, a man following a mountain path, or a man meditating in a cottage. Here the relationship between man and the natural world is the reverse of the case of Western paintings. Thus, one possible explanation for the smaller difference in the preferences of Chinese paintings is that Chinese landscape paintings are focusing on the natural scenes with human figures embedded, although small and not very prominent optically, whereas in Western landscape pictures this is rarely the case.

One important aspect which should not be overlooked is the fact that pictures in both cultures elicit the attention of the viewer. In this case we are confronted with a surprising paradox which mainly applies to Western pictures. With the central perspective in landscape paintings a wide area of the environment is represented which in reality would cover the entire visual field. In the picture, however, the visual angle is much smaller being limited to the perifoveal region. It has been shown, however, that attentional control is different for the perifoveal region and the periphery of the visual field (Bao and Pöppel, 2007); this eccentricity effect of attentional control has been well documented with a number of different experimental paradigms (e.g., Lei et al., 2012; Bao et al., 2013a). Given this situation we are confronted with a paradox: What corresponds to the visual environment in reality, and triggers the two different attentional systems, is contracted in a picture into a much smaller visual representation. This spatial contraction results in a mismatch between the natural perceptual process and its pictorial representation. What should represent physical reality, does not do it at all. On the basis of this paradoxical situation we submit the hypothesis that such a mismatch by itself leads to an external point of view. It enforces "Ich-Ferne" as this artificial perspective does not match reality. The viewer has to deal with an abstraction in the pictorial representation as has been pointed out a long time ago by Worringer (1908). Quite the contrary, the floating perspective in Eastern pictures supports "Ich-Nähe," and belongingness or embeddedness as indicated above. These different perspectives in a general sense also correlate with different cognitive strategies. The more analytical strategy corresponds to the external point of view, as the viewer is forced to take a position from the distance; the more holistic approach as has been pointed out previously (Masuda et al., 2008; Senzaki et al., 2014) is typical for the Eastern perspective, and as we want to submit being the consequence of the feeling of belongingness and the validation of personal identity. It is interesting to note that such different cognitive strategies have also been observed on a very basic level in auditory processing (Bao et al., 2013b).

Taken together, our study shows both cultural specifics and anthropological universals. Different perspectives presented in traditional Chinese and Western paintings are appreciated differently by Chinese and Westerners, showing a cultural difference in aesthetic preference. The way that artists represent the visual world in their paintings influences the way that viewers perceive their paintings. We suggest that the cultural difference in aesthetic preference is correlated with cultural and social practices in everyday life. Our aesthetic sense is to some extent modulated by the cultural environment in which we grow up. At the same time, however, results in this study indicate an overriding principle that independent of the cultural background pictorial representations of landscapes compared to people have a higher aesthetic value.

AUTHOR CONTRIBUTIONS

Study conception and design: YB and EP. Acquisition of data: QL, YF, and YW. Analysis and discussion of data: QL, TY, and XL. Drafting of manuscript: YB and TY. Critical revision: EP, YB, and QL.

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Aesthetic Experiences Across Cultures: Neural Correlates When Viewing Traditional Eastern or Western Landscape Paintings

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Compared with traditional Western landscape paintings, Chinese traditional landscape paintings usually apply a reversed-geometric perspective and concentrate more on contextual information. Using functional magnetic resonance imaging (fMRI), we discovered an intracultural bias in the aesthetic appreciation of Western and Eastern traditional landscape paintings in European and Chinese participants. When viewing Western and Eastern landscape paintings in an fMRI scanner, participants showed stronger brain activation to artistic expressions from their own culture. Europeans showed greater activation in visual and sensory-motor brain areas, regions in the posterior cingulate cortex (PCC), and hippocampus when viewing Western compared to Eastern landscape paintings. Chinese participants exhibited greater neural activity in the medial and inferior occipital cortex and regions of the superior parietal lobule in response to Eastern compared to Western landscape paintings. On the behavioral level, the aesthetic judgments also differed between Western and Chinese participants when viewing landscape paintings from different cultures; Western participants showed for instance higher valence values when viewing Western landscapes, while Chinese participants did not show this effect when viewing Chinese landscapes. In general, our findings offer differentiated support for a cultural modulation at the behavioral level and in the neural architecture for high-level aesthetic appreciation.

Keywords: beauty, cultural identity, aesthetics, visual perception, fMRI, Western painting, Eastern paintings

INTRODUCTION

Neuroscientific research on aesthetic processes in the visual system has offered evidence for a correspondence between certain properties of artworks and organizational principles in the brain (Zeki, 1999; Kawabata and Zeki, 2004; Chatterjee, 2011; Chatterjee and Vartanian, 2014; Bao et al., 2017a). Aesthetic experience partly relies on a visual analysis of an artwork based on distinct and specific visual attributes in color, line, texture, and form (Cinzia and Vittorio, 2009;

Palmer et al., 2013). Indeed, some researchers (e.g., Latto, 1995; Bao et al., 2017b) have argued that artists implicitly tap into propensities of the human nervous system when generating aesthetic appeal. Piet Mondrian's paintings are exemplary of visual art that excites orientation-selective neurons in the primary visual area. These neurons respond selectively to dots and straight lines, especially horizontal and vertical ones. Zeki's (1999) principal idea is that different kinds of artworks excite different groups of neurons in the brain, leading to differential bottom-up processes.

Drawing upon complementarity as a basic principle of biological functions (Bao et al., 2017a), aesthetic experience relies both on higher-level cognitive processes and lower-level visual analyses to enable object identification, which is necessarily both bottom-up and top-down (Zhou et al., 2016). Some of the most studied modulators of the top-down system are individual expectations, prior knowledge, social context, and cultural background (Silveira et al., 2012, 2015b,c; Graupmann et al., 2013; Leder, 2013), which also applies to other cultural domains, like poetry (e.g., Zhao et al., 2018) or even religious beliefs (Silveira et al., 2015a). It has recently been suggested that aesthetic experience is partially top–down and varies between individuals according to their cultural experience (Redies, 2015). A match of internal and external information as represented in feedforward and feedback signals of the two complementary systems plays an important role in creating perceptual stability and even pleasure (von Holst and Mittelstaedt, 1950). Human cognitive architecture is presumably built to predict representations of the world and efficiently minimize prediction errors (Clark, 2013). Conceptually overlapping with this notion, art theory describes an aesthetic experience as an interplay between internal and external perspectives (Bao et al., 2017a), i.e., by dissolving the subject/object dichotomy, the observer experiences a sense of immersion (Heidegger, 1986).

In an attempt to resolve this bi-directionality or complementarity (Bao et al., 2017a), one approach is to define an artwork as a medium capturing both an artist's understanding of a viewer's experiences and a viewer's understanding of an artist's intentions (Jucker and Barrett, 2011; Tinio, 2013). This perspective considers aesthetic appreciation to be an interaction between an artwork's objective properties and the viewer's processing characteristics of those properties. This idea is consistent with suggestions that beauty is not "put in" the artwork by the artist as a distinct entity (Zaidel, 2015), but rather "an emergent property in the brain of the beholder," where the beholder can include the artist, as well as the viewer (Redies, 2015). From a neuroimaging perspective, this phenomenon might be related to brain activation, which corresponds to the so-called mirror-neuron system and embodied simulations of emotions and actions (Freedberg and Gallese, 2007). It has repeatedly been found that positive aesthetic appreciation goes along with neural activation in parietal and sensory-motor brain regions (e.g., Lutz et al., 2013), which has been interpreted as either an empathic resonance with the painting's content or imagery and mimicry of artistic gestures. Referring back to early psychological theories, Helmholtz (1868/1995) combined the ideas that artists test and explore the visual system with a theory of vision. Artists, he claimed, are particularly good at observing their sensuous impressions (data of sensation) and at figuring out which patterns trigger which interpretations. Although many visual scientists have given up Helmholtz's theory of vision, the idea that artists test and explore the visual system has not really been abandoned (Pöppel et al., 2013). On the contrary, it allows for a more detailed and discriminating version of the same idea.

At the neural level, a considerable number of brain imaging studies on aesthetic experience demonstrate the involvement of brain regions, like the ventral striatum and medial prefrontal cortex, which are activated by reward and positive emotion (Cinzia and Vittorio, 2009; Chatterjee, 2011; Nadal and Pearce, 2011; Pearce et al., 2016). The default-mode network (DMN) is also involved when processing paintings of high aesthetic preference (Vessel et al., 2012) or of higher predictability in inferring meaningful content (Silveira et al., 2012) and has been proposed as a delayed aesthetic network (Cela-Conde et al., 2013). The DMN displays the highest activation during the resting state and task-dependent, lower activation levels (Raichle and Snyder, 2007). Overlapping with the cortical midline structures, parts of the DMN may be neural correlates for self-relevant processes. Particularly posterior parts, i.e., the posterior cingulate cortex (PCC) and adjacent precuneus, supposedly correspond to mental processes while integrating external information into a self-referential context (Northoff and Bermpohl, 2004). These processes seem to be culturally sensitive (Han and Northoff, 2008). According to recent enactive accounts of aesthetic experience (Xenakis and Arnellos, 2014, 2015), aesthetic experience arises as a result of the interaction between the viewer and the object. Aesthetic experience is also an embodied phenomenon directly linked to adaptation and aesthetic perception and helps cope with the environment. Aesthetic experience arises when the viewer interacts with both uncertain physical and cultural contexts. A more inclusive understanding of aesthetic experiences in diverse cultures has to be developed. Cultural aesthetics requires an empirical inquiry into the kinds and varieties of experiences associated with artistic activities as they are understood in different cultures.

Regarding cultural aspects, Western and Eastern artists tend to use different perspectives to represent the visual world. Western landscape paintings have been rather precise reproductions of visual surroundings since the Renaissance (Kubovy, 1986), while Eastern landscape paintings, such as Chinese paintings, have a dynamic quality that integrates successive time windows (Bao et al., 2015) and are expected to convey the experience of "being in nature" rather than "seeing nature." This has led to an arrangement of spatial information in a vertical manner with multi-layers on top of each other in a scroll form (Sullivan, 1984; Cameron, 1993; Law, 2011; Tyler and Chen, 2011). Considering cultural and historical contexts in which painting styles evolved, Western artists applied more logic and mathematics (Kline, 1964), like geometric perspective. Prevailing Buddhist and Taoist influences among Chinese artists could adequately explain the emergence of landscape painting in the Southern Song period and its persistence throughout the Ming dynasty (Golas, 2014). Besides the different artistic approaches employed by Western and Eastern painters, viewers from these two cultural groups also have distinctly different aesthetic reactions to the same artistic visual representations. Both Western and Chinese participants gave higher aesthetic ratings to paintings from their own compared to the other culture (Bao et al., 2016). One explanation might be that repeated exposure to artworks (Zajonc, 2001) promotes the development of concepts of beauty, but also of culturally transmitted values and beliefs. A given cultural value system is internalized by members of the culture, and those who internalize that system display habitual ways of thinking and behaving. Certain artworks can trigger a culturally specific feeling of identity (Pöppel, 2010). We suggest that the cultural environment in which the individual is socialized can account for the production and appreciation of art.

The current study aimed at further investigating aesthetic processes in the context of culture. We used cross-cultural neuroimaging to measure neural activity in native Chinese and Europeans living in Germany while they viewed Western and traditional Chinese landscape paintings. Based on behavioral findings of cross-cultural differences, we predicted that distinct brain-activation patterns can be observed which correspond to aesthetic preference of one's own vs. the other culture.

MATERIALS AND METHODS

Participants

Thirty-one volunteers, including 16 Europeans (7 females; mean age = 24.45 years, *SD* = 4.51 years) and 15 Chinese (8 females; mean age = 27.38 years, *SD* = 1.78 years) from the Ludwig-Maximilian University in Munich (LMU), took part in the experiment after giving informed written consent. The Chinese students are from mianland China. None of them had studied in Germany for more than 4 years when they participated in this study. All participants had normal or corrected-to-normal visual acuity and color vision, and had no history of neurological disease. To minimize the confounding effect of art education, we defined previous formal art training or art-expertise as an exclusion criteria. None of these volunteers was an art expert. Participants were asked about their preferred painting style before the experiment. They generally did not show any specific interest in a certain painting style. The study was approved by the Ethics Committee of the LMU in agreement with the Declaration of Helsinki.

Materials

Twenty-one Western oil landscape paintings and 21 traditional Chinese landscape paintings were selected from the stimuli set used by Bao et al. (2016). The stimuli set was assembled by the authors in consultation with an art specialist and was completed by using http://www.artcyclopedia.com as a search engine and was then directed to Wikimedia Commons. The contents of the landscapes mainly included the sky, mountains, rivers, trees, flowers, meadows, houses, and boats. The paintings were chosen from a variety of historical periods (from the 9th to the 18th centuries). We believe to have chosen a representative sample of paintings from the two cultural environments. All paintings were prepared in uncompressed bitmap file format, and the image dimensions varied. These paintings are referred to as Western or Eastern originals. For visual baseline, a scrambled version for each original landscape painting was created in MATLAB by dividing the original paintings into10*10 pixel units and then randomly shuffling the units to produce the scrambled stimuli. The paintings that were created using this process are referred to as Western and Eastern scrambled control condition, as they retained the overall colors of the original paintings while lacking perceptual/visual recognition. Each original painting was inverted to create an upside-down version of Western and Eastern landscape paintings. The inversion was meant to disrupt the content-related perception of the paintings. Six types of paintings were created, resulting in 126 paintings in all (see **Figure 1A**).

Procedure

All stimuli were projected onto a translucent screen through a video projector that participants could view from inside the scanner via a head-coil-compatible mirror system. A classic block design was utilized as the experimental procedure. The six types of paintings constituted six experimental conditions, each including 21 paintings separated into seven blocks. Each block consisted of three paintings of the same type; there were 42 blocks altogether. The order of all blocks was pseudo-randomized. Each block started with a fixation cross lasting for 6 s, followed by the successive presentation of three paintings. Each painting was framed on a black background and presented for 4 s followed by a 1 s interval of black screen (see **Figure 1B**). In a previous behavioral study conducted by our research group which asked participants to give ratings on beauty of Western and Chinese paintings (Bao et al., 2016), 4 s was long enough for participants to give reliable responses. Participants were instructed to view the paintings in a subjective and engaged manner, without giving any explicit response. The instruction was, "Please pay attention to the paintings shown on the screen, experience the mood of the work and the feelings it evokes, and focus on its colors, tones, composition, and shapes." To ensure sufficient attention to these paintings, participants were informed they had to fill out a questionnaire after the functional-imaging session. The decision not to collect behavioral responses in the scanner was made to facilitate maximal concentration on viewing the paintings. After the completion of the scans, each subject viewed the original paintings presented in the same block structure as in the scanner; stimulus presentation was self-paced. Participants were required to give ratings on a Likert-type Scale ranging from 1 to 7. The questions were as follows:

1. I find this painting calming (1).
   I find this painting exciting (7).
2. This painting makes me feel negative (1).
   This painting makes me feel positive (7).
3. I do not like this painting at all (1).
   I like this painting very much (7).
4. This painting is very ugly (1).

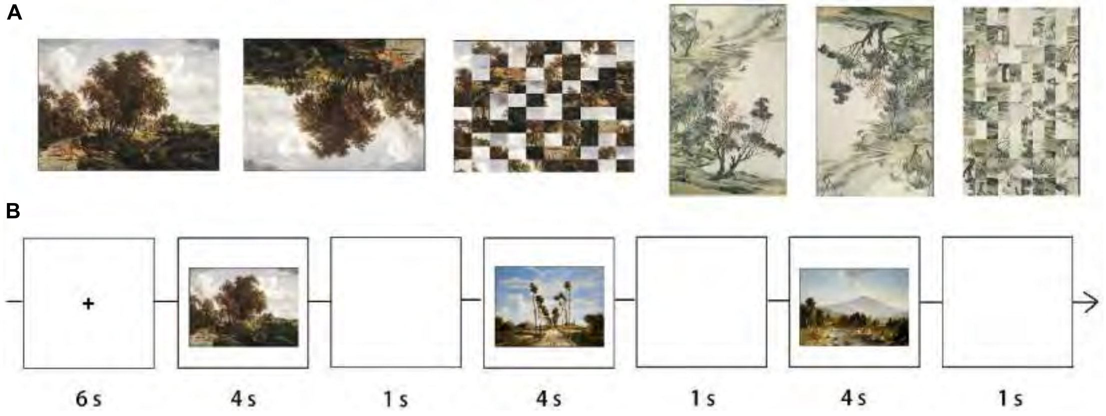

FIGURE 1 | (A) Examples of the six types of stimuli used in the experiment. From left, original Western landscape painting, upside-down Western landscape painting, scrambled Western landscape painting, original Eastern landscape painting, upside-down Eastern landscape painting, scrambled Eastern landscape painting. **(B)** A Sample block in original Western painting condition. The image stimulus duration was 4 s, with an interstimulus interval (ISI) of 1 s. A fixation cross was shown during the intervals between the blocks when no image was displayed.

This painting is very beautiful (7).

5. In the hospital, I would not like to hang this painting on the wall (1).
   In the hospital, I would like it a lot to hang this painting on the wall (7).
6. I haven't seen this painting before, and it feels unfamiliar (1).
   I have seen this painting before, and it feels familiar to me (7).
7. I don't have any feelings about this painting (1).
   I have strong feelings about this painting (7).
8. I feel like I have a distance to this painting (Outsider perspective) (1).
   I feel like I belong in this painting. (Insider perspective) (7).

The above eight questions are associated with the following mental processes, respectively: arousal, valence, preference, beauty, relaxation, familiarity, empathy, and object-related absorption. All instructions, stimulus materials, and questionnaires were given in German and then back-translated from German into Chinese by a bilingual speaker (Brislin, 1970).

Image Acquisition

Brain imaging data was obtained with a 3T MRI scanner with a standard head coil at the university hospital of the LMU in Munich. For BOLD signals, T2*-weighted EPI sequences were used [repetition time (TR) = 2500 ms; echo time (TE) = 30 ms; flip angle = 90°; acquisition matrix = 80 × 80; slice thickness = 3 mm, no gap between slices]. In total, one run of 358 functional volumes was acquired for each subject. Structural data was acquired with a T1-weighted scan of each participant's brain anatomy (1 mm × 1 mm × 1 mm; 240 × 240 matrix, field-of view = 220 mm).

Data Analysis

The behavioral data analysis was performed using SPSS for Windows (version 21.0). Paired t-tests were calculated for each question to compare the ratings on Western and Eastern paintings in European and Chinese groups separately. All neuroimaging data were preprocessed and analyzed using SPM12 (Statistical Parametric Mapping V12[1]). For each participant, the first eight volumes were removed to allow for T1-equilibration effects. The remaining 350 functional scan volumes were subjected to spatial realignment to correct for head motion. In further preprocessing analysis, the mean functional image was co-registered to the anatomical image, normalized to the Montreal Neurological Institute (MNI) template provided in SPM12, and spatially smoothed with an 8 mm Gaussian kernel.

The task was modeled as a block design. Using a two-level procedure, we conducted a random-effects fMRI data analysis. First, individual events were modeled by a hemodynamic response function. By using the general linear model, we obtained parameter estimates for each condition and each subject and then acquired statistical parametric maps of the t-statistic resulting from linear contrasts of the original and up-side-down conditions compared with their corresponding control conditions (original Western – scrambled Western, original Eastern – scrambled Eastern, upside-down Western – Scrambled Western, upside-down Eastern – Scrambled Eastern). Next, for the group analysis these individual contrast images were entered in a second-level analysis treating subjects as a random effect. The average BOLD response across the brain while viewing Western paintings was compared to Eastern paintings in both original and up-side-down conditions with paired t-tests. Reversed comparisons (Eastern paintings – Western paintings) were also conducted. For these t-tests, significant voxels initially passed a voxel-wise statistical threshold of $p \leq 0.01$, and a cluster-level threshold was obtained at the family-wise-error (FWE)-corrected statistical significance level of $p < 0.05$.

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[1] http://www.fil.ion.ucl.ac.uk/spm

RESULTS

Behavioral Results

For the European group, ratings for each question are shown in **Table 1**. Paired *t*-tests revealed that there was no significant difference between original Western and Eastern landscape paintings in average familiarity: $t(15) = 1.07$, $p = 0.301$, $ES = 0.214$. However, compared with Eastern paintings, Western paintings were rated significantly higher on valence [$t(15) = 4.01$, $p = 0.001$, $ES = 1.276$], preference [$t(15) = 3.75$, $p = 0.002$, $ES = 1.036$], beauty [$t(15) = 3.62$, $p = 0.003$, $ES = 0.938$], relaxation [$t(15) = 4.18$, $p = 0.001$, $ES = 0.842$], empathy [$t(15) = 4.84$, $p = 0.001$, $ES = 1.093$], and object-related absorption [$t(15) = 4.01$, $p = 0.002$, $ES = 0.968$], but lower on arousal [$t(15) = 2.63$, $p = 0.019$, $ES = 0.703$].

Ratings from the Chinese group are shown in **Table 2**. Paired *t*-tests indicated that preference levels and beauty levels were not significantly different between traditional Chinese and Western landscape paintings [$t(14) = 0.55$, $p = 0.58$, $ES = 0.037$; $t(14) = 1.36$, $p = 0.18$, $ES = 0.097$]. However, traditional Chinese landscape paintings had significantly higher ratings in relaxation [$t(14) = 2.50$, $p = 0.01$, $ES = 0.169$] and familiarity [$t(14) = 2.48$, $p = 0.014$, $ES = 0.143$], but lower ratings in arousal [$t(14) = 3.54$, $p < 0.001$, $ES = 0.226$] and valence [$t(14) = 5.58$, $p = 0.001$, $ES = 0.407$] compared with Western landscape paintings. There was also a marginally significant effect on empathy [$t(14) = 1.89$, $p = 0.059$, $ES = 0.145$], but object-related absorption did not reach a significant level [$t(14) = 0.84$, $p = 0.403$, $ES = 0.061$].

We performed an additional two-way analysis of variance (ANOVA) with gender as a between-subject variable for each question in both cultural groups. There was no interaction of gender by question, nor a main effect of gender (all $p > 0.1$).

fMRI Results

For each cultural group, we created whole-brain activation maps by contrasting the group-level brain response to viewing Western landscape paintings with the responses to Eastern landscape paintings both in original and in upside-down versions. European and Chinese participants exhibited distinct neural response patterns. For the European group, the analysis of original Western paintings vs. original Eastern paintings revealed a network of regions distributed across the calcarine sulcus, i.e., the primary visual area, the supplementary motor area (SMA), the PCC, the hippocampus, and the fusiform gyrus (see **Table 3** and **Figure 2**). The reverse comparison (original Western paintings vs. original Eastern paintings) revealed no significant activation. For the Chinese group, greater neural activity was observed in the right cuneus, the bilateral calcarine cortex, the left lingual gyrus, the right postcentral gyrus, and the right superior parietal lobule in response to Eastern paintings compared to Western paintings (**Table 4** and **Figure 3**). No significant activation was found in the reverse comparison (original Western paintings vs. original Eastern paintings). When comparing the upside-down Western paintings vs. upside-down Eastern paintings or upside-down Eastern paintings vs. upside-down Western paintings, there were no significant differences detected in either cultural group.

To exclude the possible confounding factor of gender, a single regressor representing the gender was added to the design matrix used in the fMRI data analysis. This revealed no statistical significance ($p > 0.1$); our data do not support that gender is correlated with BOLD responses. The differences observed in brain activations are not explained by gender.

DISCUSSION

We investigated the neural correlates of viewing Western and Eastern landscape paintings in Western and Eastern participants with fMRI. We demonstrated a cultural difference in neural responses underlying aesthetic appreciation; participants showed stronger brain activation to artistic expressions from their own cultural systems. On the behavioral level, participants from the different cultural groups expressed distinct aesthetic judgments from the two different cultures. The behavioral results, however, did not support our expectation that participants would show an overall more positive aesthetic appreciation for landscape paintings from their own culture. European

TABLE 1 | Means and standard deviations of ratings on each question for Western and Eastern landscape paintings by European participants.

	Arousal	Valence	Preference	Beauty	Relaxation	Familiarity	Empathy	Object-related absorption
Western	3.20	5.00	4.95	5.00	4.01	2.20	4.35	3.86
	(0.21)	(0.14)	(0.15)	(0.14)	(0.28)	(0.27)	(0.20)	(0.28)
Eastern	3.72	4.17	4.19	4.32	3.05	1.94	3.32	2.79
	(0.16)	(0.18)	(0.21)	(0.22)	(0.30)	(0.33)	(0.26)	(0.27)

TABLE 2 | Means and standard deviations of ratings on each question for Western and Eastern landscape paintings by Chinese participants.

	Arousal	Valence	Preference	Beauty	Relaxation	Familiarity	Empathy	Object-related absorption
Western	3.73	4.39	4.47	4.61	4.03	2.73	3.80	3.68
	(0.10)	(0.08)	(0.07)	(0.07)	(0.09)	(0.10)	(0.08)	(0.09)
Eastern	3.32	3.73	4.52	4.73	4.31	2.98	4.00	3.78
	(0.10)	(0.10)	(0.07)	(0.07)	(0.08)	(0.09)	(0.08)	(0.09)

TABLE 3 | Location of brain regions that respond to comparison of original Western paintings vs. original Eastern paintings by European participants.

Brain regions	MNI coordinates			Z scores	Number of voxels
	x	*y*	*z*		
Western – Eastern original paintings					
L Calcarine Sulcus	−9	−88	−1	4.42	246
R Calcarine Sulcus	12	−85	2	3.98	
R Paracentral Lobule	9	−28	62	3.89	442
L Paracentral Lobule	−15	−22	80	3.77	
Posterior Cingulate	0	−52	11	3.67	616
L Hippocampus	−18	−28	−10	3.67	
L Fusiform Gyrus	−30	−43	−19	3.65	

The reverse comparison (original Eastern vs. Western paintings) did not reach significance. Regions are designated using the MNI coordinates. L indicates the left hemisphere.

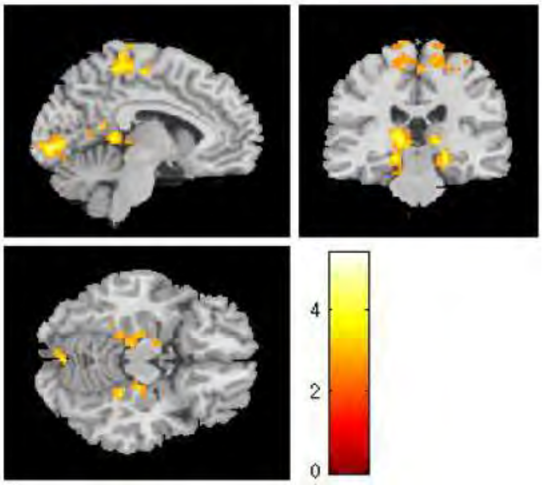

FIGURE 2 | In the European group, comparisons of the original Western vs. original Eastern paintings revealed activation in the calcarine sulcus, the paracentral lobule, the posterior cingulate cortex, the hippocampus and the fusiform gyrus.

participants rated Western landscape paintings when compared to Eastern landscape paintings higher on valence, preference, beauty, relaxation, empathy, object-related absorption, and lower on arousal. Chinese participants did not express a general preference for Eastern landscape paintings; they gave compared to Western paintings only higher ratings in the domain of relaxation. Despite the absence of a behavioral evidence of reversed aesthetic preference patterns (which does not prove the evidence of absence), we observed greater brain activation in participants for landscape paintings from their own culture. The absence of an effect when comparing the upside-down versions of the paintings highlights the content dependency of the viewed paintings. One can conclude that the observed differences are not based on bottom-up processing of the physical properties of the paintings, but that pictorial properties of the paintings extracted on a level of higher cognitive processing are responsible.

TABLE 4 | Location of brain regions that respond to comparison of original Eastern paintings vs. original Western paintings by Chinese participants.

Brain regions	MNI coordinates			Z scores	Number of voxels
	x	*y*	*z*		
Eastern – Western original paintings					
L Lingual Gyrus	−3	−85	−7	4.99	1168
R Calcarine Sulcus	−3	−94	−1	4.82	
R Cuneus	9	−94	17	4.75	
R Postcentral gyrus	33	−31	47	3.53	187
R Superior parietal lobule	33	−49	59	3.40	

The reverse comparison (original Western vs. Eastern paintings) did not reach significance. Regions are designated using the MNI coordinates. L indicates the left hemisphere.

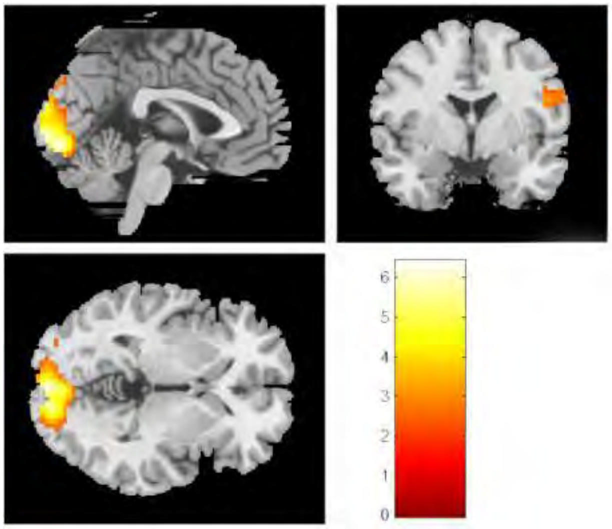

FIGURE 3 | In the Chinese group, comparisons of the original Eastern vs. original Western paintings revealed activation in the right cuneus, the bilateral calcarine sulcus, the left lingual gyrus, the right postcentral gyrus, and the right superior parietal lobe.

When the European participants viewed original Western as compared to Eastern landscape paintings, the analysis revealed higher BOLD activation levels in the primary visual cortex, the SMA, the PCC, and the hippocampus. The SMA, which has motor and sensory functions (Jeannerod, 2001), counts as one of the commonly activated brain structures when viewing artworks (Vartanian and Skov, 2014; Boccia et al., 2016). Our results correspond to previous evidence relating exposure to aesthetic vs. non-aesthetic visual stimuli to sensory-motor processes (Freedberg and Gallese, 2007; Lutz et al., 2013) and may well indicate empathic resonance with paintings from one's own cultural background. An enactive understanding of perception (Xenakis and Arnellos, 2014, 2015) suggests aesthetic behavior as emerging from the structural coupling of the viewer with his/her environment. The higher neural activation when viewing Western paintings is related to the viewer's embodiment, as posited by enactivists, and to the whole spectrum of abilities available in human socio-cultural practices.

The most likely explanation for why Western paintings elicited higher activation in the fusiform gyrus in the European group is that this structure is known to mediate object recognition. When observers view a work of art, they do not see, for instance, a canvas or a statue on an abstract level; rather, they react to what it represents (e.g., a seascape, a tower). Compared to traditional Chinese landscape paintings, Western landscape paintings have clear-cut shapes similar to hard-edge paintings. In Chinese paintings, an object's edge is ill-defined and disappears or fades into another object or into the background (Cahill, 1960; Zong, 2007). According to Wölfflin (1950), soft-edge paintings involve blurred boundaries and ill-defined forms, whereas hard-edge paintings involve well-defined forms and rich narrative details. Since the left fusiform gyrus probably plays a role in shape processing (Starrfelt and Gerlach, 2007), viewing Western landscape paintings invoked more fine-grained shape analysis than Chinese paintings, thus causing greater activation in the fusiform gyrus. This explanation is consistent with previous observations that activation in the fusiform gyrus can be attributed to object recognition in realistic paintings, including faces (Grill-Spector and Malach, 2004) and pictorial scenes (Siebörger et al., 2007).

The right cuneus, the bilateral calcarine cortex, and the left lingual gyrus were activated in the comparison of aesthetic appreciation of Eastern paintings vs. Western paintings by Chinese participants. Activation of the lingual gyrus has been linked to the encoding of complex images. Chatterjee et al. (2009) argued that activation of the lingual gyrus represents its sensitivity to "beauty," which corresponds with the present findings. Mizokami et al. (2014) showed that the left lingual gyrus and the bilateral cuneus may be associated with aesthetic judgments of representational paintings, which also supports our findings. Previous studies have related the cuneus to the aesthetic appreciation of beauty (Cupchik et al., 2009; Mizokami et al., 2014). The stronger activation in these brain structures may be explained by higher aesthetic sensitivity to stimuli with high visualization demands. Of particular interest is activation specific to the Chinese paintings localized within the calcarine sulcus corresponding to the primary visual cortex. More specifically, activation was localized to the mid- to anterior parts of the calcarine sulcus, corresponding to the mid-level and peripheral visual field representations (Sereno et al., 1995).

The higher activation levels in the primary visual cortex in both cultural groups not only indicate stronger bottom-up visual processing of paintings from one's own culture. The simultaneous involvement of the PCC in the European group, which has cortical connections to visual areas in feedforward, as well as feedback projections (Keil et al., 2009), also suggests stronger top-down processing, i.e., higher-level cortical areas modulate neural activity on the sensory-input levels. For the Chinese group, stronger activation was localized in the superior parietal lobule, a neural region known to support the manipulation of information in working memory (Koenigs et al., 2009). Top-down processes originating in superior parietal areas may contribute to the aesthetic perception of paintings and their maintenance in the "mind's eye" (Mechelli et al., 2004).

Previous studies suggested that aesthetic experience is a function of the interaction between top-down and bottom-up processing (Leder et al., 2004; Cupchik et al., 2009; Redies, 2015). However, it is difficult to delineate the exact projecting pathway of feed-forward and feedback signals with the current experimental settings. Support for a stronger involvement of top–down information processing for paintings from one's own cultural background is the additional engagement of the hippocampus, a region that has consistently been related to episodic memory retrieval (Eichenbaum et al., 1996, 2007; Brown and Aggleton, 2001). Paintings from one's own culture might be integrated into a frame of prior experiences or expectations to a higher degree due to their fit with culturally imprinted cognitive schemata, thereby linking aesthetic appreciation to one's own previous experiences. This could determine the relationship between cognition and action, thereby generating a value-oriented experience of high complexity (e.g., aesthetic appreciation), which motivates human social behavior to be related to certain types of socio-cultural expressions (e.g., appreciating or even creating/producing artworks).

We observed activation in the PCC in European participants when comparing Western to Eastern landscape paintings. This region has emerged as a key component of the DMN (Mason et al., 2007; Christoff et al., 2009; Andrews-Hanna et al., 2010), a highly interconnected network of brain regions that has been associated with self-referential mental processing (Northoff et al., 2006). More specifically, the PCC is active during tasks that involve integrating external stimuli in a self-referential manner (Northoff and Bermpohl, 2004), as well as jn autobiographical memory (Buckner and Carroll, 2007). The PCC responds to self-relevant information even when there is no explicit requirement to evaluate self-relevance (Moran et al., 2009; Reniers et al., 2012). In aesthetic experiences, individual taste in art can be considered as highly subjective, connected with personal pleasure, and can be considered a part of the personal self (Zaytseva et al., 2014). Previous research also provides evidence of higher activation levels within the DMN associated with intense aesthetic experience and interpreted as personal relevance of these stimuli (Vessel et al., 2012). When analyzing temporal dynamics of aesthetic appreciation, it has been suggested that the DMN involvement is a core part of general aesthetic experience, as represented in a delayed aesthetic network (Cela-Conde et al., 2013). The current study demonstrated that an inclusion of a cultural context was a modulator of these processes. Our results support previous findings of culturally sensitive information processing within the DMN (Han and Northoff, 2008). In Chinese group, we found evidence for increased activation in the right postcentral gyrus. This is noteworthy given that previous studies revealed the right postcentral gyrus to be activated in response to self-vs. other-perspective taking in social cognition (Ruby and Decety, 2004; Adams et al., 2010). Because the postcentral gyrus mediates somatosensory experience, the results might be explained by motor resonance created in the viewer when viewing paintings from his/her own culture. This activation, however, was not in a common area found in the previous tests of aesthetic appreciation and requires further empirical corroboration before firm conclusions can be drawn.

Why didn't Chinese participants show any activation related to self-referential information processing? There are two possible explanations. Our experimental paradigm was comparatively subtle. Pronounced cultural differences in the neural processing may emerge under more demanding conditions, verifying the expected bias of the Eastern cultural group to show preferential processing of artworks in self-related brain regions similar to the Western groups. An alternate explanation is that Asian societies are changing rapidly, and that the young Chinese participants have internalized Western values up to the point that they no longer display behavioral patterns which are characteristic for Asian cultures. Even if this is the case, the neuroimaging results clearly demonstrate different patterns for Eastern and Western participants, with a bias toward higher brain activation for one's own cultural artworks, a finding supporting the cultural/aesthetic framework proposed by Bao et al. (2016).

Our findings provide neuroimaging evidence for cultural biases in the processing of visual artworks. Visual aesthetic studies make us aware that "seeing" has a history; sensory experiences are socially, culturally, and historically embedded. It is not possible to speak of pure perception as sensation untouched by past experiences, education, and cultural background. Since our self-identity is influenced by the cultural background we inhabit, the "belonging" moments should occur with greater frequency when artists of the presented paintings and viewers who appreciate the paintings share the same cultural background. Members of different cultural groups are repeatedly exposed to various examples of visual images from their respective cultures, and they may implicitly gain knowledge (Pöppel and Bao, 2011) about the dominant aesthetic representation of the world. As mental representations of the world influence the perception of visual information, a cultural framing effect is probably implemented on the neural level and determines the implicit information processing of visual stimuli in particular and sensory stimuli in general. In this way, different cultural groups produce a "sensory model" of the meanings and values associated with their sensory perceptions. We propose that culturally distinct behaviors and thoughts can be construed as differences in aesthetic appreciation that affect neural functions. The authenticity of aesthetic experience, through its directness and immediacy, provides a powerful means of reappraising cultural experience by digging beneath the layers of accrued meanings and cognitive habits.

CONCLUSION

In conclusion, our results highlight culture as a modulating factor in the visual perception of aesthetic stimuli. Aesthetic experiences are aligned with the human cognitive architecture which is based on the principles of efficiency and prediction. This indicates a cultural framing effect, which corresponds to the mind, as well as to brain states, and determines implicit information processing. Our findings support the notion that visual experiences are biased by cultural factors. We engage aesthetically with artwork in its different expressions (e.g., visual art, poetry, music) and also with different physical environments (e.g., untouched nature, architecture, or different kinds of urban surroundings). Environments define specific perceptual features as characteristic for a particular human culture at a given time resulting in typical aesthetic appreciation. Beauty really is in the "eye" of the beholder.

ETHICS STATEMENT

This study was approved by the ethical committee of Ludwig-Maximilian University Munich, in agreement with the Declaration of Helsinki.

AUTHOR CONTRIBUTIONS

YB and EP conceived and designed the study. TY, SS, and AF acquired the data. TY and SS analyzed and discussed the data. TY and SS drafted the manuscript. MP, TS, YB, and EP critically reviewed the manuscript.

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The "third abstraction" of the Chinese artist LaoZhu: Neural and behavioral indicators of aesthetic appreciation

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Abstract: The eminent Chinese artist LaoZhu has created a homogeneous set of abstract pictures that are referred to as the "third abstraction." By definition, these pictures are meant to be representations of the artist's personal involvement and as such to create an internal point of view in the observer on an implicit level of processing. Aiming at investigating whether the artist's choice of a specific color is experienced in a specific way in the recipient, we assessed both explicit and implicit (i.e. neurocognitive) correlates in naive viewers of LaoZhu's pieces. The behavioral results reveal a preference of the original red paintings over color-changed counterparts in green or black. Paradoxically and inconsistent with predictions, we found higher levels of neural activation in several brain regions (predominantly in the frontal and parietal cortices) for the color-changed compared to the original red conditions. These observations add empirically to the complementarity of early visual pathways and higher-order cognition as well as of explicit and implicit information processing during aesthetic appreciation. We discuss our findings in light of processing effort and top-down control of the color-changed paintings. With regard to the third abstraction as defined by LaoZhu, in particular to the distinction between an external and internal point of view when viewing abstract art, our results contribute to an understanding of "abstraction and empathy" as a fundamental part of aesthetic appreciations.

Keywords: abstract art; aesthetics; color; emotion; empathy; functional magnetic resonance imaging; knowledge systems; visual art

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Single case studies are usually associated with research on a single subject, in particular patients with brain injuries or other pathologies, or a group of subjects with specific characteristics; such single case studies with patients or healthy subjects have often provided unique insights into neural and psychological processes (e.g., Bao et al., 2015; Luria, 1968; Pöppel, Brinkmann, von Cramon, & Singer, 1978; Silveira, Bao, et al., 2015; Strasburger & Waldvogel, 2015; Wang et al., 2016; Zaytseva et al., 2014; Zhou et al., 2016) and have often opened new fields of research, for instance, with respect to memory research, the famous case H.M. (Scoville & Milner, 1957). Here we expand this experimental paradigm by adopting a new strategy in relating a single person with his creative achievements in a complementary way. The artwork of the eminent Chinese artist LaoZhu on the "third abstraction" (Sun, 2011) provides a unique opportunity to follow this new line; some of his artwork is characterized by a surprising homogeneity (see his pictures from the series *Zhu Mo* in Figure S1 of the Supporting Information). This unique constellation of art and artist invites us to treat the artwork and the artist together as a "single case." Considering that paintings are the artist's expressions of inner states, the use of this strategy provides insights into common responses in several subjects and the success in transferring artistic content and meaning.

It has been suggested by LaoZhu himself that, historically, abstract art can be divided into three periods: The artworks of Wassily Kandinsky (1912/2009), Kazimir Malevich, and Piet Mondrian represent the first phase; and the cubism of Pablo Picasso and the abstract expressionism of Jackson Pollock stand for the second phase. In these first two phases, specific shapes or colors in the pictures are emphasized, forms or unique compositions with defined optical elements are dominant, and emotions may be expressed. For these two phases, one experiences or views (or even inspects) pictures preferentially with an external point of view, whereas pictures of the "third abstraction" create an internal point of view in which the personal involvement of the artist and the identification with his work is experienced by the viewer without explicit reflection but rather on an implicit level of sensory and cognitive processing (Pöppel & Bao, 2011). Art of the third abstraction as it is created and also understood by LaoZhu is strongly influenced by the typical brushstrokes from traditional Chinese art reflecting the spiritual state of the calligrapher. It captures the open-minded viewer who may feel and enjoy becoming a part of the picture; such an experience of being embedded in a picture has also been suggested when viewing Chinese landscapes, and it has been argued that such an identification with a piece of art supports personal and cultural identity (Bao et al., 2016).

What may be some critical factors that contribute to the differentiation of external or internal points of view? Such criteria may be found in "what" is represented in the picture, but also "how" the "what" is represented. We consider this distinction between the content (the what) and the way the content is represented (the how) to be crucial for a deeper understanding of an external or internal point of view and aesthetic appreciations; this conceptual (even logical) difference has been emphasized for cognitive processes in general (Bao & Pöppel, 2012; Pöppel, 1989). Without much reflection, one might assume that the content of a picture has to be dominant with respect to this question; however, a closer look at the pre-semantic level of processing appears also to be useful. In fact, substantial evidence has already been gained about aesthetic appreciations on this operational level, which may contribute also to a better understanding of these different perspectives. Not surprisingly, visual features of an artwork—such as symmetry—matter in aesthetic appreciations. Spectral analyses of different classes of visual stimuli have indicated that specific visual features of an artwork correspond to the sensory and perceptual processing in the visual stream (Graham & Redies, 2010); higher-order statistics for natural images and their usefulness for understanding visual processing in general has been demonstrated previously by Zetzsche and Krieger (2001), which may be relevant also for artwork. But simpler stimulus characteristics are also important; by swapping the colors in the tri-color compositions of Piet Mondrian's original abstract paintings, Locher, Overbeeke, and Stappers (2005) showed that manipulating the colored regions influenced the viewer's perceived weight of the areas and the judgment of the balance centers of the compositions. Thus, aesthetic appreciations of a painting may have their source in extracting basic elements of stimuli already in the early visual pathway (Cinzia & Vittorio, 2009; Zhou et al., 2016). The sensory information, derived from early and intermediate visual processing, includes color, tone (dark–light range), texture, symmetry, and contrast (Berlyne, 1971; Cupchik & Winston, 1996). But aesthetic appreciations of pictures are also controlled by top-down mechanisms, often on an implicit level (Pöppel & Bao, 2011), such as prior experiences (Silveira et al., 2012), expectations (Silveira, Fehse, Vedder, Elvers, & Hennig-Fast, 2015; Silveira et al., 2014), or the historical, cultural, and economical background in general (Jacobsen & Wolsdorff, 2007; Ritterfeld, 2002).

With respect to neural mechanisms, important observations have been made by Thakral, Moo, and Slotnick (2012), who showed that when subjects viewed paintings of van Gogh, the motion experience was associated with activity in motion-processing regions of the brain; the experience of pleasantness was associated with neural activations in the anterior prefrontal cortex, which implies that aesthetic experiences depend both on sensory processing and conceptual processing. In another study using functional magnetic resonance imaging (fMRI), Cupchik, Vartanian, Crawley, and Mikulis (2009) observed that representational paintings containing ill-defined forms elicited higher activation of the left superior parietal lobe than "hard-edge" paintings (containing well-defined forms), especially when subjects were requested to approach the paintings in a subjective and engaged manner, rather than a detached and objective manner.

Compared to representational art, abstract artwork does not consist of clearly and distinctly characterized visual objects. While the “what” diminishes in significance in most abstract artwork, the “how” rises in strength, presumably causing a perceptual bias towards basic visual elements (Aviv, 2014). Interestingly, the distinction between content (or what-functions) and logistical (or how-functions) on the neural level (Bao & Pöppel, 2012; Pöppel, 1989) finds its analogue in the historic development of pictorial art in the last 100 years. In our view, abstract art is well suited for investigating aesthetic appreciations. Particular techniques of an artist, like the manipulation of texture, color, shape, or composition, in abstract pictures can stimulate different aesthetic experiences. The present study was designed to address the modulation of aesthetic appreciation by basic visual features, focusing on LaoZhu’s abstract art. The specific choice of the color red for the brushstrokes that are meant to represent LaoZhu’s inner states was investigated in its function to transfer aesthetic appeal and artistic meaning. We examined aesthetic appreciations of LaoZhu’s original abstract paintings and color-manipulations in naive viewers, both on behavioral and neural levels. According to LaoZhu’s theory on the third abstraction, his original choice of color should lead to higher aesthetic appeal than color-changed conditions. This is assumed to be accompanied by higher neural activation in reward-related brain regions for the original color condition. A further exploratory question (which, however, can only be reflected on a speculative level) was whether the choice of a specific color as a basic sensory feature of LaoZhu’s pictures contributes to the creation of an internal, as compared to an external, point of view, thus, providing perhaps a scientific perspective to the third abstraction.

Method

Subjects

Sixteen healthy right-handed German subjects (mean age = 24.45 years, *SD* = 4.51; seven females) took part in the experiment after giving informed written consent. All had normal or corrected-to-normal visual acuity and color vision, and had no history of neurological disease. None of them was an art specialist. This study was approved by the ethical committee of Ludwig-Maximilian University (LMU) in Munich, in agreement with the Declaration of Helsinki.

Materials

Twenty-one pictures were selected from LaoZhu’s painting series *Zhu Mo* with the artist’s permission. All pictures were prepared in bitmap file format, and the image dimensions were 700 × 700 pixels. These paintings are referred to as the “original paintings.” Then we constructed the RGB image and swapped the red and green channels or removed color; the 42 paintings (21 green and 21 black) that were created through this process are referred to as the “color-changed paintings.” Scramble versions for each original and color-changed painting were created in MATLAB by dividing the picture matrix into non-overlapping blocks with the size specified by S (10 × 10 pixels), and randomly shuffling these blocks. Scramble paintings served as a control condition. The above process resulted in 126 paintings that varied along the dimensions of color (red, green, or black) and their corresponding scrambled versions (Figure 1A).

Procedure

All stimuli were projected onto a translucent screen through a video projector that subjects could view inside the scanner via a head coil-compatible mirror system. Subjects participating in the imaging study were instructed to carefully watch the paintings without giving a response. To ensure sufficient attention to these paintings, subjects were informed of the requirements of filling out a questionnaire after the functional imaging session. The decision not to collect behavioral responses in the scanner was made to facilitate maximal concentration on viewing the pictures. Paintings were presented in a block design. There were six conditions, each including seven blocks and 21 paintings; this way, each block included three paintings. The order of stimuli and blocks was pseudo-randomized. The duration of each block was 15 s. Each painting was presented for 4 s, followed by a 1-s blank screen. The inter-block interval was 6 s (Figure 1B). After the scanning session, each subject viewed the same paintings presented in the same sequence as in the scanner; stimulus presentation was self-paced. The subjects were asked “How much do you like this painting?” to which they responded using a 5-point scale ranging from 1 (*no feeling*) to 5 (*I like it very much*).

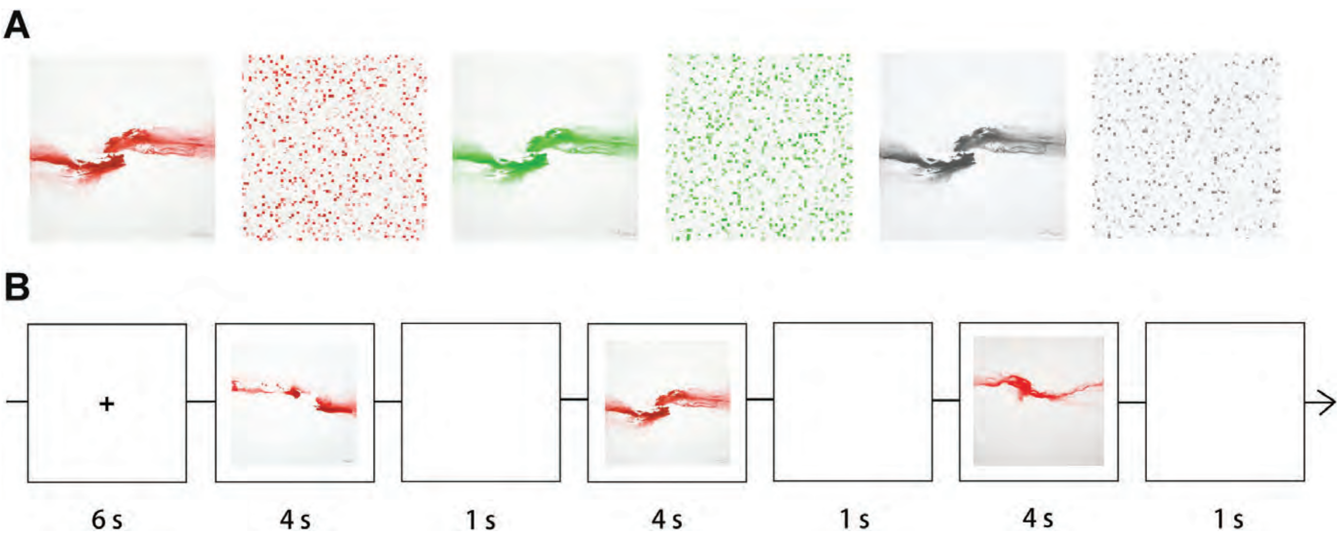

Figure 1. (A) Examples of the stimulus material used in the experiment. From left, original red, scrambled red, green, scrambled green, black, and scrambled black. (B) Experimental paradigm. Stimulus presentation was 4000 ms followed by a 1000-ms blank screen. The inter-block interval was 6000 ms.

Data acquisition

Brain-imaging data were obtained with a 3T MRI scanner with a standard head coil at the university hospital of LMU, Munich. For BOLD signals, T2*-weighted echo planar imaging was used (repetition time/echo time = 2500/30 ms; flip angle = 90°; acquisition matrix = 80×80; slice thickness = 3 mm, no gap between slices). One run consisting of 358 functional volumes was acquired for each subject. A high-resolution T1-weighted scan of each participant's brain anatomy was acquired with a 240×240 matrix, field-of-view = 220 mm, covering the brain with a slice thickness of 1 mm.

Data preprocessing and analysis

The behavioral data on liking or not liking the pictures were subjected to a one-way analysis of variance (ANOVA) with color (red, green, or black) as the variable. The data analysis was performed using SPSS for Windows (version 21.0). The MRI data were analyzed with Statistical Parametric Mapping V12 (SPM12; http://www.fil.ion.ucl.ac.uk/spm). The preprocessing procedure included removal of the first eight volumes to allow for T1-equilibration effects, 3-D motion correction by applying an affine rigid registration as part of the realignment procedure built in SPM12, and spatial smoothing with an 8-mm Gaussian kernel. In further preprocessing analysis, the mean functional image was co-registered to the anatomical image and normalized to the Montreal Neurological Institute (MNI) template provided in SPM12. Individual events were modeled by a hemodynamic response function. By using the general linear model, we obtained parameter estimates for each condition and each subject, and then acquired statistical parametric maps of the t-statistic resulting from linear contrasts between the three experimental conditions (original red, green, or black) compared with their corresponding control conditions (scrambled red, scrambled green, or scrambled black). For the group analysis these individual contrast images were entered in a second-level analysis treating subjects as a random effect. The average BOLD response across the brain in viewing original red paintings was compared to that in the other two, the color-changing conditions, with paired t-tests. For these t-tests, significant voxels initially passed a voxel-wise statistical threshold of $p \le .01$, and a cluster-level threshold was obtained at the family-wise-error (FWE)-corrected statistical significance level of $p < .05$.

Results

Behavioral results

The responses to the questions showed that the experimental manipulation by changing the colors had some important consequences. Average preference ratings for the original red paintings and their color-changed counterparts (green or black) were 4.04 ($SE = 0.11$), 3.53 ($SE = 0.09$), and 3.63 ($SE = 0.13$). The one-way ANOVA demonstrated that there was a main effect of color, $F(1, 15) = 19.648$,

$p < .001$, $\eta_p^2 = .496$, indicating a significant influence of changed colors on the aesthetic appreciations of the paintings. Bonferroni-adjusted post-hoc tests revealed that red was more preferable than green or black ($p = .002$ and $p = .011$, respectively), whereas the difference between green and black ($p = .561$) was not significant. This suggests that the subjects did not discriminate in their affective responses to the two color-changed conditions.

fMRI results

The comparison of the BOLD responses in the viewing of green paintings versus original red paintings revealed greater activations to green in several brain regions. The main clusters of an increased green-related activation were located in the left precuneus, the inferior frontal gyrus, and the inferior parietal lobules. These results are summarized in Table 1 and Figure 2. The reverse comparison revealed no significant activation.

There was also a greater activation in response to black paintings compared to the original red paintings in several brain areas, particularly in the supplementary motor area and the medial frontal gyrus. The lower parts of Table 1 and Figure 3 show a summary of these results. There was no significant activation for the reverse comparison.

Discussion

In the present study, we report the influence of color on the aesthetic appreciation of paintings by the Chinese artist LaoZhu representing the third abstraction. Both behavioral and brain-scanning methods were employed to identify potential neural correlates. The behavioral results showed that the original paintings were preferred when compared with their color-changed counterparts; surprisingly and contrary to expectation, neural activities in several brain regions which are known to be involved in aesthetic appreciations were greater when subjects looked at the color-changed paintings compared to viewing the original red paintings. Despite this discrepancy, our findings support the hypothesis that color information itself (or certain regions of the electromagnetic spectrum) can generate differential effects on neural activities when viewing abstract paintings. This may not be too surprising since specific pathways within the visual system are devoted to the processing of colors (e.g., Gegenfurtner, 2003). This functional segmentation may already be implemented at the retinal level, as experiments on color induction would suggest (Pöppel, 1986; Zhou et al., 2016). Any visual experience requires an initial analysis of optical features in the early visual pathway, and this applies also to aesthetic appreciations when viewing artwork (i.e., specific stimulus properties of perceptual objects have to be extracted). Our results add to the body of evidence stressing the importance of such primary features on the aesthetic appreciation of paintings (for a review, see also Palmer, Schloss, & Sammartino, 2013). For example, by displacing an object within original paintings, Vartanian and Goel (2004) showed that the originals were preferred compared to the changed paintings, and this comparison of original and changed pictures revealed significant activations in several relevant brain areas. Furthermore, the effects of symmetry and complexity of the stimulus configurations on aesthetic judgments have been shown to be robust in several studies (Jacobsen, Schubotz, Höfel, & Cramon, 2006; Tinio & Leder, 2009).

As indicated, our observations that color-changed artworks evoked higher neural activations are not in line with previous findings that showed higher aesthetic preferences together with higher neural activity as judged from neural processing in the reward circuitry and those neural areas assumed to be involved in the aesthetic assessment of

Table 1
Location of Brain Regions that Respond to Comparison of Color-Changed Conditions Versus Original Red Condition.

	MNI coordinates				
Brain regions	x	y	z	*Z*-scores	Number of voxels
Green–red					
L precuneus	−9	−64	35	4.68	1,092
L inferior frontal gyrus	−36	4	27	4.00	449
L inferior parietal lobule	−60	−46	38	3.94	687
Black–red					
L supplementary motor areas	−6	2	62	4.38	1,011
L medial frontal gyrus	−33	11	44	3.21	

Note. None of the reverse comparisons (red vs. green, or red vs. black) reached significance. Regions are designated using the MNI coordinates. MNI = Montreal Neurological Institute; L = left hemisphere.

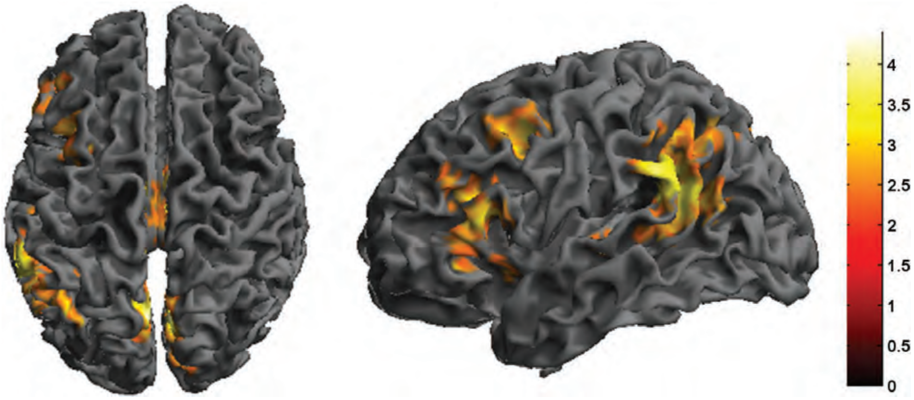

Figure 2. The green–red contrast revealed activation in the left precuneus, inferior frontal gyrus, and inferior parietal lobule.

stimuli (Lacey et al., 2011; Montague, Harvey, & Kirk, 2014). In those studies, the less preferred artworks led to less reward, less emotional valence, and less attentional orienting, all of which correlated with reduced neural activities in different brain areas. One possible explanation of our contradictory result might be that the red paintings of LaoZhu are experienced as being more natural or harmonious; the subjective experience viewing the original red paintings may require less processing effort on the neural level; such different processing effort has been suggested already in a previous study when beautiful and non-beautiful environments being stored in episodic memory were compared (Vedder et al., 2015). The color-changed versions of the pictures may result in an experiential inconsistency or a violation of a good gestalt; such a subjective inconsistency may well be implemented on an implicit level (Pöppel & Bao, 2011). The higher neural activation at the cortical level whenever a psychological mismatch, as suggested here, takes place may reflect an enhanced top-down influence. Indeed, unusual or unnatural stimuli may lead to more neural activity; for example, Kirk (2008) found that objects viewed in unexpected or abnormal figure–ground combinations led to significantly more activations compared to normal contextual conditions. More support for this notion comes also from studies when viewing abnormally colored objects (Zeki & Marini, 1998), novel stimuli (Cardillo, Watson, Schmidt, Kranjec, & Chatterjee, 2012), or irregular temporal patterns (Zeki, Hulme, Roulston, & Atiyah, 2008). Furthermore, activations were mainly lateralized to the left hemisphere in the present study, which may relate to complex, effortful processing of color-changed paintings.

In detail, the green–red contrast revealed neural activations in the precuneus, the inferior frontal gyrus, and the inferior parietal lobule. These areas are often observed as being activated in the aesthetic evaluation of artworks (Boccia et al., 2016; Vartanian & Skov, 2014). Specifically, activation of the inferior frontal gyrus may be involved in the decoding of stimuli (Kirk, 2008), whereas the precuneus, when related to vision and imagery, has been involved in voluntarily guided attention and manipulation of mental images (Cavanna & Trimble, 2006). As part of the associative cortices, the precuneus is in general related to rather abstract higher cognitive functions, in particular to an integration of external and self-generated information, which is why it has previously been linked to (1) the

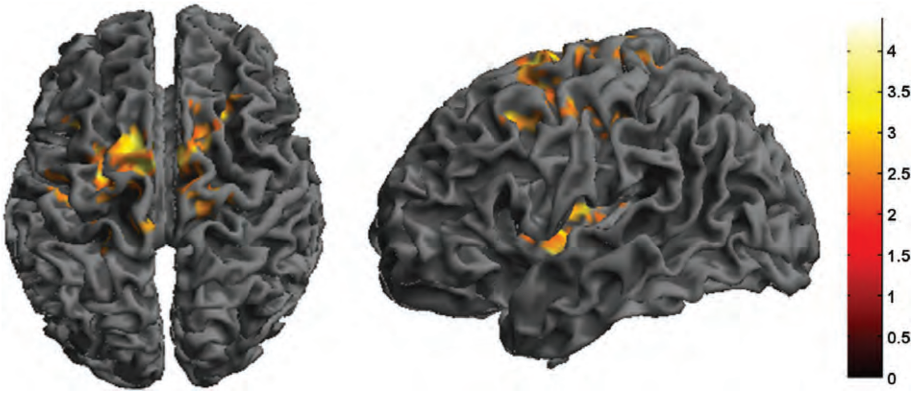

Figure 3. The comparison of black and red conditions resulted in activations in supplementary motor areas and medial frontal gyrus.

integration of external information in a self-referential context (Northoff et al., 2006), (2) the integration of egocentric and allocentric spatial relations (Cavanna & Trimble, 2006) and (3) the differentiation of first-person and third-person perspective (Vogeley et al., 2001). Thus, differential involvement of the precuneus might indicate that color modulates the strength of creating an internal point of view when observing LaoZhu’s artwork.

The direct comparison of black and red conditions resulted in activations in the supplementary motor area and the medial frontal gyrus; this observation can be related to the commonly activated brain structures when viewing artworks (Boccia et al., 2016; Vartanian & Skov, 2014). The medial frontal gyrus is likely to be engaged in higher mental functions involving executive control (Talati & Hirsch, 2005). Thus, taken together, the paradoxical result that the processing of green and black paintings compared to the original red paintings required more neural effort in the participating networks may not be at all paradoxical.

In summary, on this more technical level of analysis, the behavioral results indicate that the original red paintings of LaoZhu are preferred when compared with their color-changed counterparts, and on the neural level, higher activations for the color-changed conditions have been uncovered. These observations suggest that on the one hand, lower-level visual properties modulate the aesthetic appreciation of abstract art, but that on the other hand, higher-level neural mechanisms are also involved. This latter point invites speculation about some further aspects of our study, such as reflecting the concept of “abstraction and empathy” (Worringer, 1908/2007; i.e., the internal point of view in comparison to the external point of view) when one is exposed to pictures of the third abstraction by LaoZhu.

One question that is related to this antinomy of perspectives is why red in the pictures of LaoZhu is preferred on the subjective level than green or black. We suggest that the color red is more deeply rooted in the neural systems of humans than the other colors. Such a hypothesis is motivated, for instance, by a single case study with a patient who had suffered a bilateral occipital lobe infarction (Pöppel et al., 1978). This patient with an extremely restricted visual field had suffered a complete loss of color perception after a stroke; however, he could still differentiate between light and darkness. After some time, color perception returned to his visual world, and it was the color red that was perceived again at first. Gradually, the other colors on the perceptual level came back too; however, surprisingly green and blue could not be discriminated initially. This return of seeing colors by the patient was unrelated to retinal mechanisms that had remained intact after the stroke. This specific temporal sequence of seeing colors again after their loss emphasizes the higher importance of red, and that, indeed, red is more deeply rooted in the neural machinery of the visual system. Thus, we speculate that LaoZhu was drawn to express the third abstraction in the color red for reasons related to an ease of processing; the artist himself claims no alternative seemed suitable. This selection of the right color does not have to take place on an explicit level of rational conjecture; it happens as a self-evident process on an implicit level without necessary reflection (Pöppel & Bao, 2011). As the artist identifies himself with his own artwork, the viewer is similarly affected by the choice of “the right color.” An internal view is automatically created, and one may feel being part of the abstract scene when viewing a picture.

In fact, the viewer sees a scene and not a meaningless picture, and this makes the third abstraction of LaoZhu very different from the earlier phases of abstract art. Most of the pictures of the series studied in our experiment are characterized by a visual duality stretching along the horizontal meridian. Whatever the accidental priming of a viewer might be in a given moment, one is mentally forced (or perhaps seduced) to impose meaning onto the picture either on a concrete or a conceptual level. One person may see a landscape that might be reminiscent of a landscape picture in Eastern art (Bao et al., 2016); such “internal landscapes” may create the feeling of belongingness, again supporting and even verifying the internal point of view. Another situational priming may result in seeing red clouds in the evening sky; or one may see blood spread over a surface. On a more conceptual level, the duality of many pictures initiates a thought process about the ambivalence of life, being separated from the other and longing for togetherness.

All of these internal scenes arise automatically and without mental effort, and they touch on a fundamental principle of human knowledge systems. Other than is often implied, we do not possess just one knowledge system, which is traditionally referred to as being rational, explicit, and semantic (Descartes, 1637/1990): We possess two additional knowledge systems (Pöppel & Bao, 2011). In addition to explicit knowledge, we are in fact dominated by an implicit knowledge system that is, for instance, activated when viewing the art of the third abstraction by LaoZhu.

And we have to add a third knowledge system, which is the visual (or sensory in general) experience itself as has been stressed in particular by Zeki (1999). Seeing is knowing. Thus, when we are exposed to the third abstraction, all three knowledge systems are activated; automatically and without mental effort, both the visual and implicit knowledge systems are entrained. Then, when we reflect on what we see, or what we have seen, and when we visit our "inner museum" (i.e., the pictures that are stored in our episodic memory), we activate the explicit knowledge systems. The question remains as to whether our knowledge systems are independent of each other, or whether they are bound together in a complementary way by a common principle. It has been argued that on a conceptual level, two such unifying principles can be localized (Pöppel & Bao, 2011). In a nutshell, all knowledge obeys the mimetic principle (i.e., that knowledge is always the representation of something as something, whatever the mode of neural representation may be). Furthermore, on a formal level, the knowledge systems obey the aesthetic principle (i.e., in whatever way knowledge is represented in our neural systems or on the behavioral level, it has to please our aesthetic sense).

Disclosure of conflict of interest

The authors declare that there are no conflicts of interest.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site: http://onlinelibrary.wiley.com/doi//suppinfo.

Figure S1. Artwork of the Chinese artist LaoZhu: 21 pictures from the painting series "Zhu Mo" used in the experiments.

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Auditory perception of temporal order: A comparison between tonal language speakers with and without non-tonal language experience

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It has been shown recently that temporal order perception is modulated by language environments. The present study focused on the specific question whether a secondary language experience influences temporal order perception by comparing the temporal order thresholds (TOTs) between Chinese subjects with and without a secondary non-tonal language (i.e., English) experience. Besides monaurally presented paired clicks, binaurally presented two different types of tone pairs were used in order to better capture a potential difference between tonal and non-tonal languages. The results showed a non-significant language effect on monaurally presented click TOTs, but a significant language effect for binaurally presented tone TOTs. Compared to click performance, Chinese subjects without English proficiency demonstrated a significantly lower TOT only for close frequency tone pairs, while Chinese subjects with English proficiency demonstrated lower TOTs for both close frequency and distant frequency tone pairs. These results confirm on the one hand a common and language independent temporal mechanism for perceiving the order of two monaurally presented stimuli, and indicate on the other hand specific mechanisms of neuronal plasticity for perceiving the order of frequency-related auditory stimuli for tonal language speakers with or without a secondary non-tonal language experience.

Key words: time perception, auditory processing, order threshold, language experience

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One challenge for the human brain to understand speech is to extract the temporal order of speech sounds like different consonants and/or vowels, thus providing the operative basis for identifying phonemes, syllables, words and sentences (Pöppel 2009, Bao et al. 2013). The close link between temporal processing and language comprehension has been suggested on a theoretical level quite some time ago (Pöppel 1971, Martin 1972), and it is well established by a number of studies (e.g. Albert and Bear 1974, Tallal 2004, Szelag et al. 2011a). Evidence for such a link comes for instance from clinical studies in which parallel deficit in language and timing were reported. Deficits in speech perception at the phoneme level such as in patients with left-hemispheric lesions and aphasia (von Steinbüchel et al. 1999, Wittmann et al. 2004, Sidiropoulos et al. 2010), in children with specific language impairment (Tallal et al. 1998, Fitch and Tallal 2003), and in children and adults with dyslexia (Fink et al. 2006, Vandermosten et al. 2011, see also Szelag et al. 2010 for a review) are often associated with difficulties in processing rapidly changing auditory signals as indexed by an increased temporal order threshold (TOT) for discriminating the sequence of successively presented acoustic stimuli.

In addition to the evidence showing the connection between speech processing and temporal perception, it is also suggested that native language experience may influence auditory information processing at both behavioral and neuronal levels. Compared with English subjects, Chinese subjects who are embedded in the tonal language environment perform significantly bet-

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ter in frequency-modulated identification task (Luo et al. 2007). Furthermore, native Chinese speakers are found to be more sensitive to tone contours while native English speakers are more sensitive to early pitch differences in discriminating lexical tones (Kann et al. 2007). Brain stem responses also revealed that pitch-tracking accuracy of whole tones and pitch strength of 40-ms tonal sections were generally higher in subjects with the tonal language experience (Chinese and Tai) compared to subjects with non-tonal language experience (English) (Krishnan et al. 2010).

In a recent study (Szelag et al. 2011b) on cross-linguistic comparisons of TOTs for two monaurally presented clicks, no difference between Polish and German subjects was found across the life span from 20 to 69 years. This study seems to suggest that auditory perception of temporal order is independent of language experience. However, the absence of evidence does not prove evidence of absence; not having observed a potential language effect on temporal order perception in monaurally presented click tasks does not ensure that no such an effect can be observed in other temporal order tasks such as binaurally presented tone tasks. In addition, although German and Polish languages are different from each other, they both fall into the same category of non-tonal languages.

Unlike non-tonal languages such as English, German, Polish or Russian, the meaning of a Chinese word cannot be solely defined by phonemes without any lexical tone. For example, the Chinese syllable /fa/ has four distinct lexical meanings when spoken with different global pitch contours. It can mean ‘becoming rich’ when pronounced with a high level tone, the action of ‘punishment’ with a high rising tone, the ‘law’ with a low dipping tone, or the ‘hair’ with a high falling tone. Therefore, to extract the meaning of Chinese words, the pitch contour which features small changes in frequency range plays a crucial role. In contrast, non-tonal languages only have one single lexical meaning in one syllable regardless of some possible tone variations; thus, it is the pitch height, not the pitch contour, which is important in decoding semantic information. In other words, non-tonal languages are characterized by the large changes in frequency range, and the pitch contour plays barely any role in decoding lexical meanings.

Considering the significant difference between tonal and non-tonal languages, the present study aimed to address whether language experience influences temporal order processing by comparing the temporal order thresholds (TOTs) between tonal language speakers (Chinese) with and without a secondary non-tonal language (English) experience. In order to capture the possibly higher sensitivity of Chinese subjects to small changes in frequency range featured by pitch contour, we applied not only monaurally presented clicks as stimuli but also binaurally presented two different types of tone pairs as stimuli. One is “close frequency” tone pairs using 600 Hz and 1 200 Hz tones as stimuli; the other is “distant frequency” tone pairs using 400 Hz and 3 000 Hz tones. If a common temporal mechanism exists for click TOT as suggested by Szelag and coauthors (2011b), then no difference on click TOTs should be observed between the two subject groups. Since monaurally presented clicks might not be appropriate for capturing a potential language effect on temporal order perception as has been shown previously (Bao et al. 2013), the main focus of the present study is to possibly reconfirm the previous observations and to further examine whether the experience of a secondary non-tonal language (i.e., English) may improve the TOT performance on the “distant frequency” tone task. As a selective impact of tonal and non-tonal language environment on TOT performance of tones has already been demonstrated (Bao et al. 2013), i.e., Chinese subjects tend to show lower TOT for close frequency relative to distant frequency tones, while Polish subjects demonstrate the opposite, we expected in the present study that Chinese subjects without English proficiency would show a lower TOT only for close frequency and not for distant frequency tones as compared to click TOT, while Chinese subjects with English proficiency would show lower TOTs for both close frequency and for distant frequency tones.

Eighteen native Chinese speakers without proficiency of a non-tonal language (NC group) and 18 native Chinese speakers with proficiency of English (NCE group) participated in the present study. All subjects were college students. They speak standard Mandarin as well as one local Chinese dialect and have no experience of other languages except English. The subjects of the NCE Group had passed the formal College English Test 4 (CET, Band IV) at the National Ministry of Education in China. All participants were right-handed (Oldfield 1971) and had no history of neurological or psychiatric disorders, or any indication of cognitive impairment. None of the participants had

Table I

Detailed characteristics of participants

Group	*n* (Male/Female)	Age Range (Years)	Mean Age (SD)	Handedness (Left / Right)	Mosaic (SD)	Hearing Status (Normal /Not)
NC	18 (9/9)	20–29	25 (2.4)	Right	37.4 (7.3)	Normal
NCE	18 (9/9)	19–27	23 (1.8)	Right	37.8 (5.8)	Normal

(NC) native Chinese speakers without proficiency of a non-tonal language; (NCE) native Chinese speakers with proficiency of English; (*n*) number of participants; (SD) standard deviation

received a formal musical education, which possibly could increase the sensitivity of auditory perception of acoustic stimuli.

To ensure normal hearing for all participants, pure-tone audiometry screening was assessed (Audiometer GSI 17). Participants with hearing thresholds higher than 30 dB HL and differences of more than 20 dB HL between the two ears were excluded from the study (ANSI 2004). In all participants intellectual abilities were assessed (nonverbal Mosaic Test, see Tewes 1994) and matched scores were obtained for the two groups. Detailed descriptive data of the participants are listed in Table I.

The stimuli were paired sounds presented in rapid succession with varied inter-stimulus-intervals (ISI, i.e., the time distance between the offset of the first stimulus and the onset of the second stimulus). Three types of paired stimuli were used in the study: paired clicks, paired close frequency (600 Hz and 1 200 Hz) sinusoidal tones, and paired distant frequency (400 Hz and 3 000 Hz) sinusoidal tones. The clicks were 1 ms rectangular pulses presented in an alternating monaural stimulation mode, i.e., one click was presented to one ear, followed by another click to the other ear. Subjects were asked to indicate the sequence of the two clicks by pointing to one of the two response cards: “left-right” or “right-left”. The tones were generated with the program Cool Edit 2000 (sampling rate 44 100 Hz, 16-bit), and each tone lasted 10 ms with 1-ms rise-and-fall time. The paired two tones in each trial were presented in a binaural stimulation mode, i.e., each tone was presented to both ears with a short gap in between. The subjects had to indicate the temporal order of the two tones by pointing to one of the two response cards: “low-high” or “high-low”.

In all measurement, the stimuli were presented *via* headphone (SONY MDR-CD 480) at a comfortable listening level which is well above threshold. The inter-stimulus intervals between the two acoustic stimuli were controlled by a maximum-likelihood based algorithm – YAAP procedure (Treutwein 1997). According to the subjects’ previous responses, the ISI of the present trial was set at the current best estimate of the threshold corresponding to 75% correct responses based on a logistic psychometric function. The main measurement for each type of stimuli was preceded by a practice session in which participants reported the temporal order of the two acoustic stimuli presented with a constant, relatively long ISI of 160 ms. The practice was continued until a criterion of 11 correct responses in a series of consecutive 12 presentations was reached.

The sequencing ability was indexed by the temporal order threshold (TOT) which was defined as the minimum time interval required for correctly identifying the temporal order of two successively presented stimuli. To obtain individual values of TOT, a logistic psychometric function was fitted to the subject’s data, using MATLAB toolbox psignifit version 2.5.41 (see http://bootstrapsoftware.org/psignifit/), a software package which implements the maximum-likelihood method described by Wichmann and Hill (2001). This procedure estimates an inter-stimulus interval (ISI) corresponding to 75% correct order discrimination (Strasburger 2001). The click TOT was calculated by the estimated ISI plus the duration (1 ms) of the first click, and the tone TOT by the estimated ISI plus the duration (10 ms) of the first tone, thus both using SOA (stimulus onset asynchrony, the time interval between the onset of the first stimulus and the onset of the second stimulus) as TOT index.

A two-way mixed ANOVA was performed for the values of TOT with Stimulus Type (clicks, close frequency tones, and distant frequency tones) as a within-subjects variable and Subject Group (NC group, NCE group) as a between-subjects variable. The results showed a significant main effect of stimulus type and a non-significant main effect of subject group, $F_{2,68}=21.531$, $P<0.001$, $\eta_p^2=0.388$, and $F_{1,34}=1.563$, $P>0.05$, $\eta_p^2=0.044$. More importantly, the stimulus type significantly interacted with subject group, $F_{2,68}=3.467$, $P<0.05$, $\eta_p^2=0.093$. Further analysis of this interaction using *t*-tests with Bonferroni corrections revealed very interesting TOT patterns: For the NC group, a significantly lower TOT was observed for discriminating the temporal order of the two close frequency tones relative to both the clicks (31 ms vs. 56 ms, $P<0.01$) and the two distant frequency tones (31 ms vs. 54 ms, $P<0.01$), and no TOT difference between the clicks and the distant frequency tones was observed (56 ms vs. 54 ms, $P>0.05$). However, for the NCE group, although a similar high TOT was observed for the clicks as compared to the NC group (63 ms vs. 56 ms, $P>0.05$), both the close frequency tones and the distant frequency tones resulted significantly lower TOTs relative to their click TOT (21 ms vs. 63 ms, $P<0.001$; 34 ms vs. 63 ms, $P<0.01$). No TOT difference between the two types of tones was observed (21 ms vs. 34 ms, $P>0.05$) (see Fig. 1).

The present study measured temporal order thresholds with both monaurally presented clicks and binaurally presented two types of tones in both NC and NCE subject groups. The results of click TOT confirmed previous observations (Szelag et al. 2011, Bao et al. 2013), i.e., no TOT difference between NC and NCE groups was observed. Thus, the click TOT results suggest a general phenomenon in temporal order processing, i.e., a common and language independent mechanism underlying milliseconds timing which governs monaurally presented click ordering.

With the substitution of frequency-related tones for clicks and the more natural mode of stimulus presentation, namely, binaural instead of monaural presentation of the stimuli, a more sensitive measurement was involved to capture a language effect on temporal order perception. As the TOT results of the two different types of tones indicated, the NC group showed a significantly lower TOT for discriminating the temporal order of two close frequency tones, while the NCE group demonstrated significantly lower TOTs for both the close frequency and the distant frequency tones. These results are consistent with our predictions based on the major difference between tonal and non-tonal languages. Since tonal language speakers like Chinese were experienced with pitch contour detection in their natural language environment, they were more sensitive to small changes in frequency range, thus a lower TOT for close frequency tones relative to distant frequency tones was observed for the NC group. As non-tonal languages are characterized by large changes in frequency range, being exposed to such a language like English apparently increases the sensitivity to large changes in frequencies, thus improving the NCE subjects' temporal order processing of two distant frequency tones.

The language impact on tone TOT performance in the two subject groups can also be interpreted with reference to two different strategies used for temporal order perception (Bao et al. 2013). As already known, both analytic and holistic strategies can be used for decoding the sequence of two acoustic stimuli. When the analytic strategy is used, a subject has to identify the singular acoustic events in their identity and on that basis experiencing directly the temporal order of the two events. For example, in the TOT measurement with tones, the two successively presented tones were of different frequencies: one was a low frequency tone, and the other was a high frequency tone. Thus, the tone order judgment involves not only a temporal order task, but also a frequency discrimination task. Therefore, the subjects may identify the frequency of

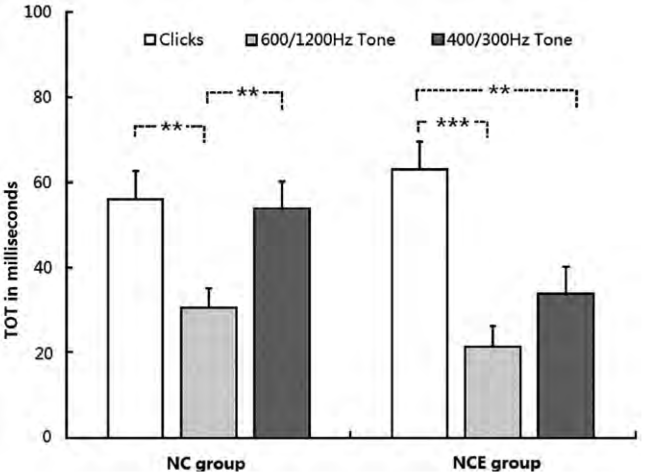

Fig. 1. Temporal order thresholds (TOTs) measured for clicks and two types of tone pairs (600/1 200 Hz and 400/3 000 Hz) in two subject groups. The "NC group" represents native Chinese speakers without proficiency of a non-tonal language, and the "NCE group" represents native Chinese speakers with proficiency of English (**$P<0.01$, ***$P<0.001$).

each tone immediately following the presentation of the individual stimulus, and on that basis report the temporal order of the two tones. When a holistic strategy is used, the two successively presented frequency-related tones are integrated into one unitary percept with either an up or a down patterning. On the basis of such global patterning, subjects reconstruct secondarily the temporal order of the two stimuli, leaving the identification of each individual tone unnecessary (Brechmann and Scheich 2005, Szymaszek et al. 2009). Compared to the analytic strategy, the holistic strategy usually leads to a lower temporal order threshold.

For native Chinese subjects who were experienced in detecting pitch contours, they might use a holistic strategy for perceiving the temporal order of two close frequency tones and an analytic strategy for the two distant frequency tones, thus showing lower TOT for close frequency tones relative to distant frequency tones. In contrast, for native Chinese subjects who were experienced also in a non-tonal language, it could be that being exposed to a non-tonal language their analytic strategy was shifted to a holistic one for decoding the temporal order of two distant frequency tones. The holistic processing mode being shaped by tonal or non-tonal language environment seems to be consistent with previous studies using single neuron recording technique, which suggest that neurons in the primary auditory cortex are selective to directions of frequency modulated sweeps (e.g., Tian and Rauschecker 2004). Possibly, such neurons are differently stimulated when being exposed to a tonal or a non-tonal language. The flexible holistic processing tuned by a tonal or non-tonal language experience suggests neural plasticity of the auditory brain as suggested previously (Merzenich and Sameshima 1993).

In conclusion, the main results of the present study indicated a clear impact of language experience on temporal order perception: While native Chinese speakers without English proficiency were good at discriminating the temporal order of two close frequency tones, native Chinese speakers with English proficiency were good at both the close frequency and the distant frequency tone order discrimination. Combining the similar performance for click order perception in both subject groups, a selective modification of language experience on temporal order perception is suggested in the present study.

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Donders revisited: Discrete or continuous temporal processing underlying reaction time distributions?

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Abstract: Differences of reaction times to specific stimulus configurations are used as indicators of cognitive processing stages. In this classical experimental paradigm, continuous temporal processing is implicitly assumed. Multimodal response distributions indicate, however, discrete time sampling, which is often masked by experimental conditions. Differences in reaction times reflect discrete temporal mechanisms that are pre-semantically implemented and suggested to be based on entrained neural oscillations.

Keywords: discrete time sampling; excitability cycles; ex-Gaussian distribution; intrahemispheric learning; neural oscillations; processing stages; reaction time

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Some 150 years ago, Donders published one of the most important methodological papers in experimental psychology (1868/1969). He introduced the paradigm of reaction time differences to analyze cognitive processes, and he also stressed the importance of single case studies. The “Donders method” led to important concepts, like the suggestion of sequential processing stages (Sternberg, 1969), or the discovery of the eccentricity effect of attentional control in the visual field (Bao & Pöppel, 2007). In spite of the usefulness of this paradigm, the question has to be raised as to whether the underlying theoretical assumption holds true that temporal processing is of a continuous nature. This implicit assumption is never explicitly expressed, but it follows from the statistical treatment of reaction time distributions, which are considered to be unimodal. To give just one example, Whelan (2008) states:

> Response times are not Gaussian (normal) distributions but rather rise rapidly on the left and have a long positive tail on the right … Reaction-time distributions are similar to the *ex-Gaussian* distribution … which is a convolution (mixture) of a Gaussian and an exponential distribution that has been shown to fit empirical distributions well. (p. 475)

Along with other theoretical distributions that have been considered (like lognormal or Gamma distributions), such an ex-Gaussian distribution is unimodal, and unimodality implies that a reaction can be initiated at any time after stimulus occurrence; thus, temporal processing has to be continuous within this theoretical frame.

The focus only on unimodal distributions is surprising because unimodality is often violated when measuring reaction times. Multimodal distributions have been observed many times (e.g., Harter & White, 1968; Pöppel, 1970). It is rather a technical question as to why multimodal distributions are often not observed, and there are several reasons why multimodal distributions may escape attention. A trivial reason is that the temporal sensitivity for measuring reaction times may not be sufficient; for example, if different modes in distributions are separated by some

30 ms, they obviously cannot be observed in measurements with temporal bin widths of 20 ms or 30 ms, or even longer bin widths. More important reasons for not observing multimodal distributions are the instationarity of experimental conditions that comes about in many disguises: Subjects in an experiment may still be in a learning phase not having reached a plateau of performance. It takes thousands of trials when measuring choice reaction time to reach such a plateau (Pöppel, Schill, & von Steinbüchel, 1990). Another reason for violating stationarity is that experiments are done at different times of day, neglecting the importance of circadian phases (Pöppel & Bao, 2014). Furthermore, multimodality can also be masked if measurements from different subjects are superimposed; even small individual temporal differences between neighboring modes may simulate a unimodal distribution when integrated within one histogram. To demonstrate the importance of these technical points, we use some observations that have been described in detail some time ago (Pöppel et al., 1990) in which different types of distributions are disclosed, shedding new light also on perceptual learning.

In a long-term experiment lasting for 8 weeks, intrahemispheric visual and auditory choice reaction times were studied in three young adult subjects; here we show data from just one subject (female, 25 years) for auditory choice reaction time. In the experiments, visual stimuli were presented at 4-deg eccentricity to the right of the visual axis; auditory stimuli were presented by earphone to the right ear. Within one experimental session, 250 visual and auditory stimuli were presented with equal probability in random order. To prevent fatigue, after 25 trials, a rest was provided, and all measurements were taken at 9:00 a.m. To further reduce variance, reaction times were recorded as "go-reactions," that is, the release of the right index finger from a testing button towards one of the two response buttons, and the correct button had to be pressed as quickly as possible after the appearance of a visual or an auditory stimulus, thus, preventing the influence of the movement time towards a response button. Following an outlier analysis, approximately 120 measurements within each session and for each modality remained to construct the statistical distributions for each day (Figure 1). We show four results from different phases of the experiment that indicate unique patterns of response distributions (indicated also as red cartoons).

Figure 1A shows the distribution of measurements at the beginning of the experiment with a mode at about 300 ms and with high temporal variability, which might be modeled as a Gaussian distribution. Such a distribution may be representative for typical experiments when inexperienced subjects without an extended learning phase participate in behavioral studies. At a later phase of the experiment after some sensorimotor learning has taken place, a completely different pattern is observed (Figure 1B); the distribution becomes bimodal with much shorter reaction times for the first and also for the second mode in the distribution. To model these observations with a Gaussian or ex-Gaussian unimodal distribution would be misleading. After more repetitions, a unimodal distribution develops that is skewed to the right (Figure 1C); this distribution can indeed be

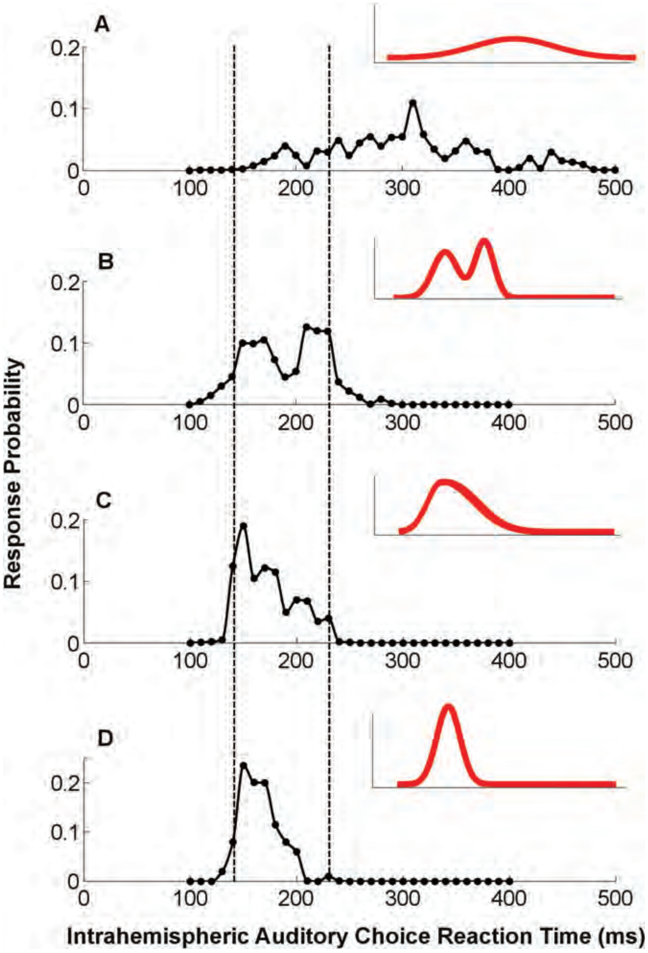

Figure 1. Distributions of auditory choice reaction time selected from a long-term experiment with one subject; abstracted distributions in red (adapted from Pöppel et al., 1990; for details see text). Bin width of measurements was 10 ms. (A) Initial measurement, modeled as a Gaussian distribution. (B) Bimodal distributions appear by the second measurement. (C) A rightward-skewed unimodal distribution develops with the seventh measurement, modeled as ex-Gaussian. (D) Final measurement after 8 weeks is again modeled as Gaussian.

modeled to be ex-Gaussian. Finally, after even more experimental sessions under identical conditions, a unimodal distribution is observed (Figure 1D) which, however, is fundamentally different from the first distribution (Figure 1A), although it may be modeled also as a Gaussian distribution. It should be noted that approximately the same location in the empirical distributions at about 150 ms for the first peak in Figure 1B and the peaks in Panels C and D are observed, indicating long-term stability in temporal processing after the initial instability.

This experimental sequence observing stationarity for measurements shows that statistical distributions of choice reaction time exhibit fundamentally different patterns. The bimodality after an initial learning phase (Figure 1B) with some 60 ms between the peaks suggests excitability cycles as hypothesized some time ago (Pöppel, 1970); sensory stimuli entrain neural oscillations and the initiation of reactions is controlled by specific phases of these oscillations. Thus, a reaction cannot be triggered on the neural level at any time as unimodal distributions would imply; on this basis, one has to conclude discrete time sampling of information processing. It has to be emphasized within this conceptual frame that the periodic processes represent neural "relaxation oscillations," which are instantaneously entrained by stimuli; this is different from neural oscillations, which do not allow phase-resetting by sensory stimuli. Furthermore, they are of a pre-semantic nature (Pöppel & Bao, 2014), that is, processing stages are not defined by the information processed, but discrete temporal windows are used to process information. This mechanism also sheds some new light on the question as to when processing stages have come to an end. The fact that bimodality is shifted to unimodality in this individual case (Figure 1D) does not contradict the proposed mechanism of discrete time sampling; sensorimotor learning may result in higher efficiency of stimulus processing focusing on the read-out of sensory input to one time window only. With respect to the "subtraction method" introduced by Donders, it has to be concluded that discrete time sampling may be masked by experimental conditions in which stationarity for measurements is violated. It is recommended that when analyzing cognitive processes, the evidence of discrete time sampling is acknowledged, and that statistical distributions are modeled according to the observed data.

Disclosure of conflict of interest

The authors declare that there are no conflicts of interest.

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When is the right time? A little later! Delayed responses show better temporal control

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Abstract

Human behaviour is characterized both by action and reaction; the action mode can be conceived of as being embedded in anticipatory control, whereas the reactive mode requires the instantaneous processing of stimuli. In the reaction mode, tasks have to be completed (most of the time) as fast as possible; in the action mode, the task is to act “at the right time” anticipating the consequences of one’s actions. A control machinery for the action mode has been suggested some time ago by the “reafference principle” (von Holst & Mittelstaedt, 1950), the theoretical concept already being formulated by Ernst Mach and Hermann von Helmholtz in the 19th century. The basic idea is that an action program not only initiates a motor program, but an efference copy is drawn from this program, which is compared after the completion of the movement with the re-afference. When efference copy and reafference match, the movement program is cancelled, i.e., the movement has come to an end. There are plenty of examples to support the basic notion of the re-afference principle, but there remains one essential shortcoming, i.e., the temporal domain. The re-afference principle is conceived of as being temporally neutral which is both theoretically and practically not satisfying. How can one test temporal constraints that might shed some more light on behavioural control?

Quite often, observations from everyday behaviour may provide an incentive for experimental paradigms. Everybody may have been confronted with the feeling that a planned action with an anticipated movement pattern is experienced to happen at the wrong time; sometimes one acts too early and sometimes too late, the reason often being that the attentional control was disrupted. Examples can, for instance, be observed in driving an automobile (Tanida & Pöppel, 2006) or in some sport activities like football, tennis or squash. Practical experience shows that it is often necessary to delay an action for better temporal control. We decided on the basis of theoretical considerations and practical experiences to look into this temporal control problem in more detail by examining delayed actions using a modified experimental paradigm of a previous experiment (Szelag et al., 2001).

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Participants were asked to respond to visual targets presented continuously with pre-defined delays between 400 and 5000 milliseconds; ten such different delays were chosen (400, 600, 800, 1000, 1500, 2000, 25000, 3000, 4000, 5000 ms). For each delay time, 40 trials were sequentially employed, and after each trial the participants was provided a feedback of the response time. The goal of the participants was to delay the action as accurately as possible. A critical variable was also the standard deviation (SD) of the 40 trials for each pre-defined interval being normalized; i.e., each SD was divided for comparison reasons by the average response time to the target delay time. As a control the fastest reaction times for each subject were also measured. The results are quite clear and surprising: Participants were very fast to adjust their response time to the pre-defined delay time; the best response time was actually observed for the longest delay time with an average of 4992 ms for 5000 ms delay time. More interesting, however, were the results for the normalized SDs: The largest value with some 60 ms was observed for the shortest delay time of 400 ms. These normalized SDs became smaller for the longer delay times being characterized an exponential decay and reaching a plateau of some 20 ms at approximately 3000 ms delay time. As 40 trials were employed, it was possible to compute the normalized SDs for the first and second 20 trials; it turned out that there was a clear learning effect, i.e. the second 20 trials showed much smaller SDs for all pre-defined delay times. The fastest reaction with on average 220 ms was much shorter than the selected delay times, thus, lying outside the operating range of the pre-defined delay times.

The higher variance for shorter delay times comes as a surprise and might even be considered to be a paradoxical phenomenon. One might expect for shorter delay times smaller variances compared to longer delay times, but the contrary is the case. Better temporal control is reached if the "waiting time" is extended beyond the temporal limit of approximately three seconds. If attention is focused on the passage of time, an optimal action mode is switched on only after a few seconds; our experiments do not indicate how long such an anticipatory "temporal window" may last. But what the experiment indicates is that up to such an optimal delay time responses are characterized by temporal instability. It appears as if between fastest reactions and optimal actions our behaviour is characterized by a "temporal twilight" zone. If this is a case as the data indicate, it certainly makes sense to delay actions for some time, in case a fast reaction is not required.

These observations also shed new light on basic features of the re-afference principle. If actions cannot be precisely pre-programmed because their execution shows too high temporal variance, the "efference-copy" is not clearly defined. This temporal instability makes it next to impossible to match the efference-copy with the re-afference; this then results in behavioural instability. Only if sufficient time is allowed to pass may such a match between anticipation and satisfaction become operative.

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Keywords: Delayed responses; reafference principle; reaction time; anticipation; movement control

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Synchronization as a biological, psychological and social mechanism to create common time: A theoretical frame and a single case study

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Abstract: Synchronizing neural processes, mental activities, and social interactions is considered to be fundamental for the creation of temporal order on the personal and interpersonal level. Several different types of synchronization are distinguished, and for each of them examples are given: self-organized synchronizations on the neural level giving rise to pre-semantically defined time windows of some tens of milliseconds and of approximately 3 s; time windows that are created by synchronizing different neural representations, as for instance in aesthetic appreciations or moral judgments; and synchronization of biological rhythms with geophysical cycles, like the circadian clock with the 24-hr rhythm of day and night. For the latter type of synchronization, an experiment is described that shows the importance of social interactions for sharing or avoiding common time. In a group study with four subjects being completely isolated together for 3 weeks from the external world, social interactions resulted both in intra- and interindividual circadian synchronization and desynchronization. A unique phenomenon in circadian regulation is described, the "beat phenomenon," which has been made visible by the interaction of two circadian rhythms with different frequencies in one body. The separation of the two physiological rhythms was the consequence of social interactions, that is, by the desire of a subject to share and to escape common time during different phases of the long-term experiment. The theoretical arguments on synchronization are summarized with the general statement: "Nothing in cognitive science makes sense except in the light of time windows." The hypothesis is forwarded that time windows that express discrete timing mechanisms in behavioral control and on the level of conscious experiences are the necessary bases to create cognitive order, and it is suggested that time windows are implemented by neural oscillations in different frequency domains.

Keywords: beat phenomenon; circadian rhythm; desynchronization; discrete time; social interaction; synchronization; time window

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Frame of reference

Modern biology is guided by a principle that has been summarized by Dobzhansky (1973) with the memorable sentence: “Nothing in biology makes sense, except in the light of evolution.” On the basis of this conceptual frame, we both generalize and also suggest more specifically that nothing in neurobiology, psychology, the social sciences (or cognitive science in general), makes sense except in the light of synchronization, that is, the creation of common time for temporally and spatially distributed sources of information or events. Without synchronization, neural information processing, cognitive control, emotional relations, or social interactions would be either impossible or severely disrupted; without synchronization we would be surrounded by informational chaos, desynchronized activities, unrelated events, or misunderstandings. Synchronization as a fundamental principle is implemented on different operating levels by temporal windows with different time constants (Pöppel & Bao, 2014). Temporal windows are the basis for the creation of perceptual, conceptual, and social identity (Zhou, Pöppel, & Bao, 2014), and they provide the necessary building blocks for the construction of experiential sequences, or for behavioral organization. Thus, we reformulate: “Nothing in cognitive science makes sense except in the light of time windows.”

When referring to temporal windows, it is necessarily implied that information processing has to be discontinuous or discrete. Although of fundamental importance, the question of whether information processing on the neural or cognitive level is of a continuous or of a discrete nature has not received sufficient attention in research; for instance, in experiments using reaction time as a chronometric indicator in cognitive tasks, continuous processing of information is taken for granted (see, however, Fingelkurts & Fingelkurts, 2006; Pöppel, 1997; VanRullen & Koch, 2003). The implicit assumption of a continuous processing mode of information may be due to an unquestioned orientation of psychological reasoning towards classical physics. This is how Isaac Newton (1686/1969) defines time: “Absolute, true, and mathematical time, of itself, and from its own nature, flows equably without relation to anything external.” With this concept of an “equal flow,” time serves as a unidimensional and continuous “container” within which events are happening at one or at another time. Does this theoretical concept of temporal continuity provide a solid conceptual background when we want to understand neural and cognitive processes? The concept of temporal windows that are suggested to be implemented by neural or bodily oscillations in general, and which can be considered to be the operative basis for synchronization on the level of neural, behavioral, and experiential organization, speaks against such a frame of reference. As will be demonstrated, temporal processing has to be necessarily discrete to allow for efficient complexity reduction of sensory information on different operating levels. Before describing a single case study as a paradigmatic example, we provide some arguments (mainly from our own research environment) that prove synchronization as a fundamental principle.

Temporal processing units

Access to the environment is obviously gained through our sense organs. In spite of the triviality of this statement, the fact has to be realized, however, that the transduction mechanisms are qualitatively different in different sense organs as reflected in their time constants. The transduction process in the auditory system is much shorter compared to the visual system; it takes less than a millisecond at the receptor level in the auditory modality, but some tens of milliseconds in the visual modality. Furthermore, light and sound take different amounts of time to reach an observer; whereas the speed of light is irrelevant under ecological conditions, the time it takes for a sound to reach an observer has to be taken into account. Under optimal conditions (for the visual modality) a “horizon of simultaneity” is located at an approximately 10-m distance, when the time it takes for the sound to reach an observer corresponds to the transduction time for optical stimuli to be transduced at the retina (Pöppel, Schill, & von Steinbüchel, 1990). More complicated are non-overlapping routes for transduced signals to travel to central processing areas in different sensory modalities. If auditory and visual information have to be integrated, as for instance to identify a person or an object in one’s personal environment, the brain is confronted with a logistical problem as persons or objects are not tagged with respect to their distance, and neural signals are not necessarily marching in lockstep. To overcome this logistical problem of integrating information from different sensory modalities, the neural machinery has implemented system states or processing units within which sensory information is treated as co-temporal, that is, as if they would have happened at the same time. Empirical evidence shows that such processing units within which afferent information is synchronized have a duration of some tens of milliseconds (Pöppel, 1997). One important implication of such an integrating and synchronizing activity is that temporal continuity within this time window from the perceptual viewpoint does not exist; a before–after relationship of information is not defined within a temporal processing unit. Physically non-synchronous events are synchronized on the neural level to allow complexity reduction, and on that basis the definition of “primordial events” has been suggested (Pöppel & Bao, 2014).

Experimental support for a time window in this temporal domain comes from a large number of different paradigms on the behavioral and physiological level. One such paradigm is to measure the temporal order threshold in different sensory channels, that is, how much time it takes to define an event as such, and to localize it in a perceptual sequence. It turns out that the temporal order threshold is similar in different sensory modalities (Hirsh & Sherrick, 1961). This suggests a central and not a peripheral neural mechanism of processing. The temporal order threshold can, however, be modulated within limits by long-term imprinting (Bao, Szymaszek, et al., 2013; Bao et al., 2014) or short-term priming (Liang, Zhang, & Bao, 2015). Other experimental support for this time window comes from multimodal histograms of reaction time or from latency measurements of eye movements; the modes in response histograms are separated by some tens of milliseconds, which suggest central excitability cycles (Pöppel, 1970; Pöppel & Logothetis, 1986). It has to be concluded that a response cannot be initiated at any point on an axis of continuous time, but that it is controlled by a temporal machinery that allows a response or an action only in discrete sequential steps. In a theoretical analysis, it has been shown that the concept of a “traveling moment” as it has already been implied by James (1890) cannot be held upright; on the basis of experimental evidence, it has to be concluded that sensory stimuli entrain an oscillatory process, and it is suggested that one period of such an oscillation serves as the operative basis for a time window within which information is integrated.

Oscillations in the temporal domain of some tens of milliseconds have also been observed on the physiological level. Single-cell recordings in the visual pathway, like in the lateral geniculate nucleus, show stimulus-triggered oscillations with periods in this time domain (Podvigin et al., 2004; Podvigin, Jokeit, Pöppel, Chizh, & Kiselyeva, 1992). Similarly, in the auditory modality the midlatency response of the auditory evoked potential is characterized by an oscillatory component in the same frequency range (Madler & Pöppel, 1987; Schwender, Madler, Klasing, Peter, & Pöppel, 1994). More importantly, general anesthetics suppress this oscillatory component, and patients who undergo an anesthesia report that no subjective time at all has passed after they wake up again. Thus, it can be concluded that neural oscillations in the temporal domain of some tens of milliseconds provide the functional basis for this time window; if the oscillations are suppressed, as in anesthesia, the time window is suppressed with the consequence that no sensory information can be integrated in an appropriate way, and a loss of consciousness ensues.

A time window of 3 s

One important characteristic of the time window for the processing units mentioned above is that they are implemented pre-semantically. Thus, it is not the information itself that creates the time window, but the neural machinery that provides the time window to be used for the representation of information independent of the content to be processed. Because of this distinction, temporal information processing can be referred to as a logistical function (the “how” of processing) compared to content functions (the “what” of experiences) as has been suggested in a taxonomy of functions (Bao & Pöppel, 2012; Pöppel, 1989a); this distinction between the two functional domains proves to be useful within the context of modern “connectomics” and a better understanding of psychiatric and neurologic diseases (Zaytseva, Chan, Pöppel, & Heinz, 2015). Such a pre-semantic implementation applies also for a time window of approximately 3 s (Pöppel, 1997, 2009). Abundant evidence shows that the brain provides a temporal platform that is used in visual and auditory perception, movement control, sensorimotor synchronization, speech segmentation or attentional modulation, and even in cultural artifacts, like in music (Pöppel, 1989b) or poetry (Turner & Pöppel, 1988).

The recently discovered eccentricity effect on attentional control in the visual field (Bao & Pöppel, 2007) is one example of a time window of a few seconds. Using the paradigm of inhibition of return (IOR) it has been demonstrated that spatial attention is modulated differently for the perifoveal compared to the peripheral region of the visual field; the IOR effect is significantly stronger in the periphery, which is associated with a more prominent projection of the periphery to the superior colliculus of the midbrain, whereas the perifoveal region shows a more prominent projection via the lateral geniculate nucleus to the visual cortex. Although the IOR effects are based in different neural networks (Lei, Bao, Wang, & Gutyrchik, 2012), the two attentional systems share the same time window (Bao, Wang, et al., 2013) proving the power and apparent necessity of temporal integration to create unity in cognitive processing.

Such a unity can be violated, as has been demonstrated in patients with brain injuries or in autistic children, and the violations can be considered as proof of their existence. In patients with injuries in the left hemisphere resulting in a "Broca aphasia," the time window of 3 s is impaired, resulting in alternative strategies to integrate sequential information into perceptual units or a gestalt compared to the effortless temporal integration observed in healthy controls (Szelag, von Steinbüchel, & Pöppel, 1997). Furthermore, in a task to reproduce temporal intervals, it has been observed that stimulus durations up to approximately 3 s are reproduced veridically with small variance, whereas longer intervals will be reproduced shorter and with higher variance, suggesting a different gain function (e.g., Pöppel, 1971). Some autistic children show a very different pattern of temporal reproduction, that is, they have a tendency to reproduce any interval with approximately 3 s independent of stimulus duration (Szelag, Kowalska, Galkowski, & Pöppel, 2004). This unique behavior observed in single cases allows a direct look into the temporal machinery of the brain; apparently, some autistic children (as perhaps also some schizophrenic patients with formal thought disorder) can no longer modulate an endogenously implemented temporal integration process, that is, the disease uncovers the eigenoperations of the temporal machinery as the patients seem to be "frozen in time."

Although most evidence for a time window of 3 s comes from behavioral studies, a recent study has provided direct evidence on the neural level, supporting the concept of a pre-semantic integration mechanism (Wang, Lin, Zhou, Pöppel, & Bao, 2015). Using mismatch negativity (MMN) as an indicator, it was tested whether a time window of 3 s is particularly sensitive for detecting the violation of the regularity in a stimulus sequence by employing different inter-stimulus intervals. The results show that in frontal midline areas, the amplitudes of the MMN are significantly larger for inter-stimulus intervals up to 3 s than for the longer inter-stimulus intervals. It can be concluded that a time window of 3 s is selective for pre-attentively processing sensory information in a privileged way and that information processing is temporally segmented, implementing in discrete sequential steps operative platforms for the creation of perceptual and conceptual identity and a "subjective present" (Pöppel & Bao, 2014; Zhou, Yang, Zhang, Zhang, & Mao, 2015).

The time window of 3 s also plays an important role in sensorimotor synchronization (Mates, Müller, Radil, & Pöppel, 1994; Miyake, Onishi, & Pöppel, 2004). If subjects are asked to synchronize a regular sequence of auditory stimuli with defined movements like finger taps, they can do this with small temporal variance only up to approximately 3 s. If the next stimulus to be synchronized with a motor action is beyond this time window, precise anticipation is no longer possible. With longer intervals between successive stimuli, anticipation of what is going to happen is replaced by a reaction; one has to "wait" for the next stimulus, which cannot be anticipated any more with temporal precision. This time window in sensorimotor synchronization is fundamental for interpersonal communication because it provides a common time window within which effortless prediction and sharing of social intentions becomes possible. It has been demonstrated that human speech is also segmented with time windows of a few seconds (Vollrath, Kazenwadel, & Krüger, 1992); this allows for the creation of common time in verbal communication, and such common time can also be considered as an operative basis for an emotional link between partners as their endogenously generated rhythms are synchronized.

Operational and conceptual time windows

The time windows of some tens of milliseconds and of a few seconds described above are expressions of self-organizing principles of the human brain. In the context of our reasoning, they appear to be necessary for complexity reduction of information, and they represent the neural basis for the creation of identity on the perceptual and cognitive level (Pöppel, 2010; Zhou et al., 2014). On different operative levels, temporally distributed information is automatically integrated or synchronized; pre-semantic processes provide temporal platforms for the creation of content. Thus, the cognitive machinery is driven by neural mechanisms that are outside conscious control. These time windows represent the logistics of the brain as suggested in a pragmatic taxonomy of functions that is based on neuropsychological and psychiatric observations as well as evolutionary considerations (Pöppel, 1989a; Zaytseva et al., 2015). The general concept of time windows and synchronization applies, however, to two more functional domains: (1) synchronization of behavior with geophysical cycles, like the 24-hr rhythm (as described in the single case study below); and (2) operational and conceptual time windows within which distributed information is synchronized to give rise to distinct phenomena on the experiential level. A typical example for such time operational windows are aesthetic appreciations or moral judgments (Avram et al., 2013, 2014; Pöppel et al., 2013; Vedder et al., 2015).

In experiments on aesthetic and moral judgments using functional magnetic resonance imaging (fMRI), the neural networks of both judgment types have been compared (Avram et al., 2013). It was observed that both aesthetic and moral judgment share the same neural network, however, with one important difference: Moral judgments use the same neural areas, including the posterior cingulate cortex, the precuneus, and the temporoparietal junction. Thus, what appears on the subjective level as different cognitive acts, like aesthetic and moral judgments, share a common neural basis. It has to be concluded that moral judgments require an aesthetic component in their neural implementation; possibly, this aesthetic component in moral judgments reflects the search for coherence in cognitive processing, or the "good" is synchronized with the "beautiful" on the neural level.

A similar phenomenon of sharing different representations by synchronization can be observed in neural mechanisms underlying the appreciation of artwork. It has been shown that the brain distinguishes effortlessly between naturalistic and surrealistic pictures, as if the neural structures are equipped with a mechanism to recognize without reflection between what is physically possible and what is impossible (Silveira et al., 2012). However, with a death prime, this neural difference characterizing naturalistic and surrealistic pictures is significantly modulated (Silveira et al., 2015). The prime seems to create a new neural frame of reference. This modification of the neural responses after a defined prime (as a death prime in this case) is only possible if within a time window of finite duration the prime modulates neural activities in a top-down manner.

An equivalent mechanism of neural modulation within a time window has to be assumed in music perception. It has been shown that musical training elicits a higher sensitivity to detect sadness in speech (Park et al., 2015). This observation implies that long-term exposure to music modulates the neural threshold in emotional sensitivity, but this long-term effect becomes real only in a given moment when being exposed to expressed sadness in speech. The importance of a situational context has also been demonstrated for temporal perception (Zhou et al., 2015). Thus, long-term experiences as represented in the mnemonic systems and short-term primes modulate the synchronization of past and present representations. These effects from the recent and not so recent past (e.g., Vedder et al., 2015) on present conscious states can be considered as empirical evidence for the synchronization of temporally distributed information within one time window; thus, synchronization is the necessary mechanism to integrate past and present representations.

One of the most challenging questions in cognitive science is to understand the basic mechanisms of personal identity or one's own self. It has been suggested that midline structures of the brain are essential, as has been verified for instance in a single case study with a professional singer (Zaytseva et al., 2014). The direct comparison between listening to her own voice compared to someone else's voice showed a relative activation of precuneus, visual cortex, posterolateral thalamus, and cerebellum in the perception of self. Referring to oneself is necessarily a subjective phenomenon in a present moment, although this may happen on an implicit level, that is, self-confirmation does not have to take place on an explicit level (Pöppel & Bao, 2011).

The creation and confirmation of personal identity on a phenomenological level can also be linked to being one's own doppelganger (a "copy of oneself"), as recent research results and theoretical considerations suggest (Pöppel, 2010). This hypothesis is based on observations from episodic memory with subjects of different ages and sexes. If subjects time-travel to their personal past as represented in their episodic memory, they spontaneously report that in images of the past they "see" themselves as an agent, as if they were their own doppelganger. This doubling must be based on an active process of the human mnemonic system, that is, to project an image of oneself into the pictorial representation from the past. Thus, no image in the episodic memory represents physical reality; images of the past are completely individualized and, only on a superficial level, there may be a correspondence of elements if several observers have been exposed to the same pictorial scene. This projection of oneself into images of the past has an important psychological consequence: Being one's own doppelganger makes it possible for anybody to refer to oneself. This self-reference is an implicit process in the present, but it can be made explicit if, under conscious control, we time-travel to our own past as it is represented in episodic memory. That is to say, the episodic memory provides an efficient way by bringing the past into the time window that represents the "present" (Zhou et al., 2014) to synchronize the past and present "selves," thus giving rise to a coherent and subjectively continuous self-identity through the lifespan. On that basis, it follows that the tragedy of a memory loss is mainly the loss of a potential and necessary self-reference (Han et al., 2014). Without the reference to the past in the synchronized present, a patient does not know any more who he or she is, because the patient has lost the doppelganger in the personal mirror of his or her episodic memory. Thus, the synchronization of past images within a time window in the present can be considered as representing a neural basis of personal identity.

A temporal bridge between past experiences as being projected into present experiences is obvious for any kind of cognitive processing; we want to point out, however, that such time-encompassing links require synchronizing mechanisms, and these are necessarily embedded within time windows. Experimental evidence suggests (as described above) a time window of a few seconds that serves as a logistical basis for integration. What is represented within such a time window is, however, not independent of what has been represented before; what will be represented in the next time window is determined or modulated by what is represented in a present time window. Anticipation of what comes next, and the dependence of present experiences of what has been, reflect another binding mechanism of the brain, that is, the semantic connection of successive representations. This semantic connection of what is represented in successive time windows can also be considered as an explanation for the phenomenal continuity of time, which has to be understood as an illusion, although as a necessary illusion (Pöppel & Bao, 2014). On the level of neural activities, temporal processing requires time windows of finite duration, and they express discrete timing mechanisms of the brain; on the phenomenal level of temporal experiences, we fall victim to semantics, as the continuity of meaning shadows the underlying neural processing. Connecting the content of successive time windows of approximately 3 s is itself an active neural process as reflected for instance in listening to music (Park et al., 2015), possibly based on the longer time constants of emotional processing. Such a hypothesis can be derived from observations with neuropsychiatric cases, like patients with schizophrenia, in whom the continuity of semantic processing may be disrupted.

Circadian time windows

Evolutionary adaptations to geophysical cycles

It is useful to distinguish on the time axis between two domains of temporal control, that is, on the one hand self-organized mechanisms as mainly exhibited for short-term intervals in the sub-second to minutes domain (see above), and on the other hand long-term mechanisms as observed in circadian or circannual rhythms reflecting evolutionary adaptations to geophysical cycles. It is an open question whether the processes of temporal control across the temporal domains are interdependent, thus, reflecting one mechanism, or governed by independent operative principles. It has been argued that one common underlying mechanism may indeed be possible (Agostino, Golombek, & Meck, 2011).

Research on circadian rhythms has shown that human behavior is controlled by an endogenous mechanism (Aschoff, 1965) that is indicated by free-running periods, that is, rhythms under constant conditions are no longer exactly 24 hr corresponding to the geophysical cycle. An endogenously controlled mechanism can also be suspected for annual cycles (Roenneberg & Aschof, 1990). For circadian rhythms, it has been shown that they can be synchronized only within a limited range of entrainment that is not too different from exactly 24 hr (Aschoff, Pöppel, & Wever, 1969); this observation supports the concept of a genetically controlled time window that is experienced as a day and matches approximately the rotation of the earth; otherwise synchronization to any zeitgeber ("time-giver") would be possible. It is interesting to note that circadian clocks are observed for most light-sensitive organisms, from unicellular organisms to humans (Roenneberg & Merrow, 2005). A common evolutionary background allows us to study principal questions on circadian rhythms with model organisms like *Gonyaulax polyedra* or *Neurospora crassa* (Merrow et al., 2003), and in particular to analyze mechanisms of entrainment that apply across species (Roenneberg, Daan, & Merrow, 2003; Roenneberg, Dragovic, & Merrow, 2005). Thus, all these organisms share the same time window created by the adaptation to the rotation of the earth. Circadian rhythms are characterized by a specific pattern of neural activations (Blautzik et al., 2013) and dysregulations, as observed in neuropsychiatric cases (Blautzik et al., 2014; Monti et al., 2013; Wulff, Gatti, Wettstein, & Foster, 2010), which allow us to better understand the underlying control mechanisms.

In addition to the light–dark cycle as the dominant zeitgeber to synchronize the 24-hr period of rest and activity with the geophysical cycle, social interactions, or the social environment in general, have also been shown to play a role in entrainment (Honma et al., 1995; Mistlberger & Skene, 2004; Wittmann, Dinich, Merrow, & Roenneberg, 2006). It was found, for instance, that blind subjects can use social cues to entrain their circadian rhythms (Klerman et al., 1998). However, it has also been claimed that for humans, social signals are unable to cause mutual synchrony in constant conditions (Davidson & Menaker, 2003). This contradicts results that, under complete isolation, social synchronization of circadian rhythms is possible (Aschoff et al., 1971; Pöppel, 1968). Here we report observations on synchronization and also desynchronization of circadian rhythms in a group of completely isolated subjects; some results on physiological functions have been reported previously (Pöppel, 1968). As will be described on the basis of data obtained from a single case, social interactions can be a powerful tool to get a unique insight into the temporal machinery of circadian rhythms and their interactions with short-term timing.

Synchronization and desynchronization of functions in a single case

Experimental situation

Four young male subjects were isolated completely from the environment for 3 weeks without any access to external information. Subjects lived in two connected experimental rooms underground (a "bunker"), and they did not have any knowledge about the time of day; there was no direct contact with the external environment and the subjects did not have watches. Light intensity in the experimental space chamber was 1400 Lux during the first half of the experiment and 100 Lux during the second half. Light was continuously switched on, and the subjects could decide for themselves when they wanted to get up or go to sleep. Before this group experiment, the subjects had participated in an experiment with individual isolation; thus, they were already used to the specific experimental conditions. During the individual isolation, the four subjects showed free-running circadian rhythms with the following periods: 24.4 hr (Subject S), 24.6 hr (Subject B), 24.9 hr (Subject K), and 25.1 hr (Subject M).

The goal of the group study was to investigate whether living with others would lead to behavioral synchronization of the circadian rhythms. Would the subjects exhibit the same rhythm, or would everyone follow his own rhythm as observed previously? Another question was whether in case of social synchronization the group rhythm would be shorter compared to the average of the individual rhythms. This question was based on the hypothesis that social interactions may increase the level of activation for all subjects, which secondarily could speed up the circadian clock. To answer these questions, the rest–activity cycle was measured separately for each subject, and in addition, body temperature during the sleep phase and kidney functions were monitored as indicators of diurnal variations. All urine samples were collected from each subject to determine volume and concentration of different electrolytes (sodium, potassium, calcium). The subjects also had to perform several tests throughout their subjective day (always after having delivered a urine sample), such as the production of 10-s intervals, or they had to indicate their "personal tempo," that is, tapping with their fingers at a comfortable and self-selected speed.

Before the experiment, several psychological tests (German standardization) were taken independently to gain general information about the personal profiles of the subjects. These tests showed that Subject S had the highest IQ with 130 compared to 112 (Subject B), 112 (Subject K) and 120 (Subject M). Measurements with a test on "vegetative lability" gave the following results: 27 (Subject S), 9 (Subject B), 10 (Subject K), and 10 (Subject M); and measurements with a test on "neuroticism" gave the following results: 17 (Subject S), 7 (Subject B), 10 (Subject K), and 5 (Subject M). These measurements showed that Subject S was possibly a psychological outlier or a "critical case" with highest values in intelligence (130), vegetative lability (27) and neuroticism (17). Thus, from the psychological point of view, the isolated group was not a homogeneous sample with Subject S as a potentially interesting single case.

Physiological and psychological results

The rest–activity cycle of the four subjects showed both synchronization and desynchronization (Figure 1). In the first part of the experiment, the rest–activity cycle of the four subjects was synchronized with a circadian period of 26.2 hr. The critical case S, however, showed an important phase difference compared to the other subjects, starting his subjective day on average 2 hr earlier, although the beginning of the sleep phase was synchronized with the other subjects. After the first half of the experiment, light intensity was reduced from 1400 Lux to 100 Lux. After this change, the subjects continued to live in a synchronized manner for a few

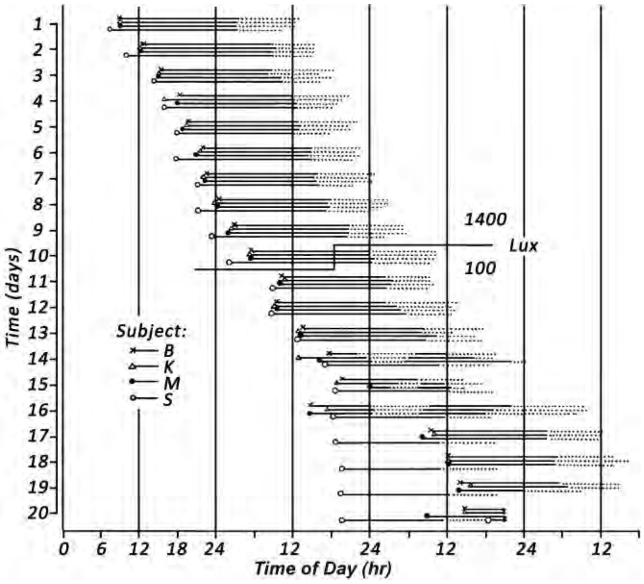

Figure 1. Rest–activity cycle of four male subjects being isolated together for 3 weeks under constant conditions. Lines represent time being awake, dotted lines being asleep. Light intensity in the first half of the experiment was 1400 Lux and 100 Lux in the second half. On successive days indicated from top to bottom the four subjects were synchronized with each other in their rest–activity cycle in the first half of the experiment, but no longer in the second half, although their synchronized period was no longer 24 hr. In the first half of the experiment, one subject (S) started his phase of wakefulness on average 2 hr earlier than the three other subjects.

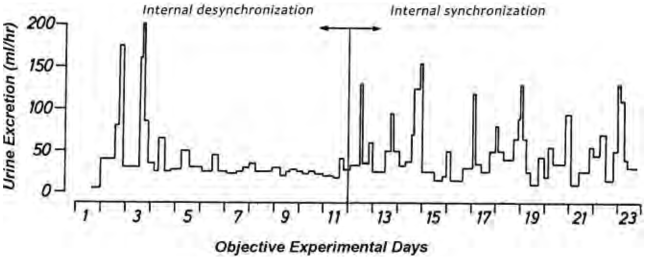

Figure 2. Diurnal pattern of excretion of urine in one subject (S) participating in a group experiment with four subjects. The different diurnal patterns for the first and the second half of the experiment indicate "internal desynchronization" for the first (suggesting a beat phenomenon) and "internal synchronization" for the second half of the experiment (for details see text).

more days. From day 13 until day 16 of the experiment, the first signs of an interindividual desynchronization could be observed. All subjects, except the critical case S, took a midday nap for a few hours. From day 17 until day 20 of the experiment, the critical case S no longer lived in synchronization with the other subjects. At this point, he had a much shorter subjective day (on average 24.1 hr) compared to the other subjects, who lengthened their circadian day in synchrony to as long as 27.2 hr.

Under normal circumstances, the diurnal cycle of urinary excretion is synchronized with the activity cycle. Interestingly, this was not the case with the critical case S in the first half of the experiment (Figure 2). On the first 2 days of the experiment, distinct daily maxima were observed, but the range of amplitude got smaller until a diurnal rhythm was no longer visible. Only shortly before the change of light intensity, the rhythm of urinary excretion as an index of kidney functions reappeared; this applied both to volume and the electrolytes measured in the urine samples. During the second half of the experiment, the expected diurnal pattern was observed until the end of the experiment. Measurements of body temperature of the critical case S during sleep showed also that he deviated from the other subjects. His body temperature increased at the beginning of the experiment, it remained at the higher average level of 36.9 °C for a longer time, and it decreased again to a lower average value of 36.2 °C when he desynchronized with his rest–activity cycle from the other group members. Thus, during this phase of the experiment, the body temperature of the critical case S during his sleep phase corresponded to an expected lower value similar to the values of the other subjects.

Other unexpected results were obtained with the measurements of temporal production. Before the group experiment started, each subject went through a learning phase to produce as accurately as possible a 10-s interval without counting. All participants reached within a few trials a reliable set point with only small variance (Figure 3). During isolation, each subject selected within several days of transitions rather different individual set points when producing the 10-s intervals; one subject produced the target interval on average with approximately 6.5 s (M), another one with 8.5 s (B), a third one with 11 s (K), and the critical case S with 16 s. Thus, no correlation was observed between the periods of the individual circadian rhythms and the temporal production of the four subjects. Interestingly, the critical case S with the shortest circadian rhythm showed the longest temporal production, supporting the hypothesis of independent mechanisms for short-term temporal control and long-term circadian organization.

While the experiment on temporal production showed high interindividual variance, a rather different observation was made when measuring the personal tempo (Figure 4). During the experiments of individual isolation, each participant had selected a different personal tempo with intervals between successive taps of approximately 0.2 and 0.8 s; for the critical case S, the period was on average 0.55 s for successive days. During the group experiment, an unex-

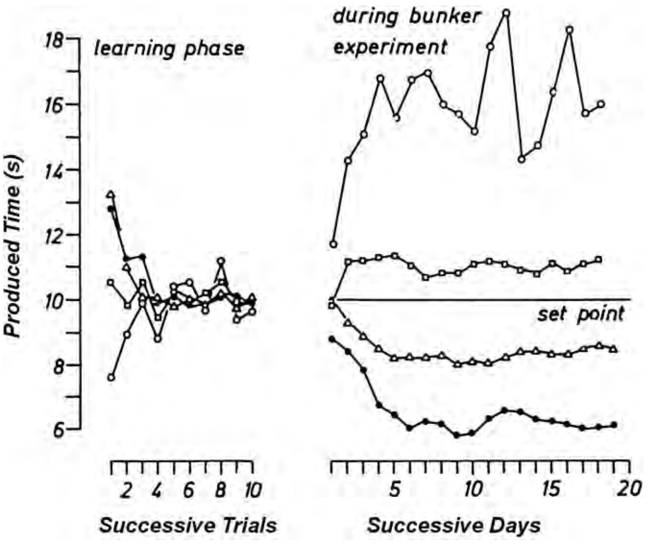

Figure 3. Results of temporal production of a 10-s interval by four male subjects during an initial learning phase (left side) and during complete isolation. During the learning phase, when the subjects received feedback about their performance they were finally quite accurate in producing a 10-s interval; however, during the bunker experiment, after 1 or several days, every subject selected a personal interval that was different from the learned set point.

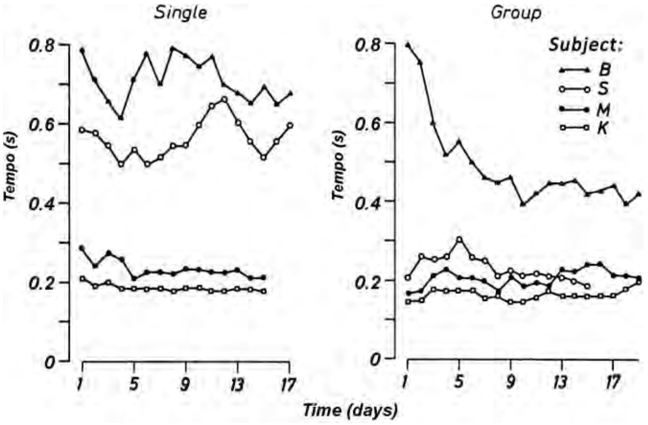

Figure 4. "Personal tempo"—an individually selected speed of finger tapping with a comfortable tempo—of four subjects during two experiments of complete isolation. Left: Results from individual (single) isolation for several days. Right: Results from an experiment with common (group) isolation. During common isolation, three subjects exhibited a rather similar tempo with one subject (S) instantaneously adapting to the tempo of two other subjects, which was very different from the personal tempo of individual isolation, whereas one subject (B) after a phase of transition of several days, adapted to approximately half the tempo of the other three subjects.

pected social synchronization occurred: Three subjects, including the critical case S, selected a personal tempo with intervals close to 0.2 s, that is, they selected approximately the same high-frequency tempo. Subject B, who had selected the rather slow tempo with intervals of 0.8 s in the individual experiment, changed his personal tempo in the group within several days to a value close to intervals of 0.4 s, which corresponds approximately to a harmonic value of the other subjects being half as fast compared to the others. Thus, an effect of social synchronization could be demonstrated also on short-term timing.

Discussion of synchronization and desynchronization

The measurements of the rest–activity cycles of the four subjects indicate that social synchronization is possible, thus, contradicting previous claims (Davidson & Menaker, 2003). This is even possible if some effort is required as in the case of the critical case S; at the beginning of the experiment, this subject forced himself to live in synchrony with the other subjects although his own circadian clock might have preferred another rest–activity cycle. This behavior as an expression of a possible desire to be synchronized with others and sharing the same time window might be explained by a need for social comfort. Furthermore, the results show that the social synchronization of the circadian rhythms towards a mean value of 26.2 hr (first half of the experiment) and 27.2 hr (second half of the experiment) argues against the hypothesis that social synchronization results in shorter rest–activity cycles under free-running conditions when compared to values obtained under individual isolation.

Several surprising results were obtained with the critical case S both in long-term circadian timing and short-term temporal production and personal tempo. They indicated both the desire to belong to the group by synchronizing the rest–activity cycle and adjusting the personal tempo, and also the desire to escape by finally choosing a different circadian rhythm. The much longer intervals for temporal production compared to the other subjects also support the hypothesis that the critical case S was an outlier on both the physiological and psychological levels; this, however, allowed deeper insight into the circadian machinery and the relationship between long-term and short-term timing. As for the latter, it appears to be unlikely that timing in the sub-second and second range are controlled by the same mechanisms as has been suspected (Agostino et al., 2011).

Of particular interest is the rest–activity cycle of the critical case S, who was synchronized with the other group members in the first half of the experiment. This period of 26.2 hr was apparently too long for other physiological functions to be synchronized. The phase difference observed in the critical case S indicates that his circadian clock had a tendency for a shorter subjective day compared to the others.

This could be proven by the circadian modulation of the vegetative functions as represented for instance by the kidney functions. Most surprisingly, the circadian modulation of the kidney functions disappeared a few days after the beginning of the experiment, but reappeared spontaneously after several days. This suppression of the circadian modulation can be interpreted as a beat phenomenon. Thus, social synchronization of the critical case S resulted in an internal desynchronization, which became observable through the beat phenomenon. Two circadian clocks were running at the same time, one superimposed by the group and one dominated by the individual circadian clock resulting in the beat. A support for this interpretation is provided by the second half of the experiment when the critical case S no longer lived in synchronization with the group but followed his own temporal schedule close to 24 hr, whereas the other three group members extended their circadian day in synchrony to as long as 27.2 hr. In this second half of the experiment, the critical case S no longer exhibited an internal desynchronization. To the best of our knowledge, such a beat phenomenon with two superimposed circadian cycles in one person has never been observed before. What are some psychological implications of this unique behavior? The critical case S, who could be described as highly neurotic but also highly intelligent, had been eager to adapt initially to the rest–activity cycle of the other subjects. However, this desire to adapt in time and thus socially belong was apparently not appreciated by the other subjects who classified him as an outsider. The negative attitude of the other subjects might explain the desynchronization of the critical case S in the second part of the experiment when he escaped into his own time window.

This study shows that living in an isolated group under constant environmental conditions can lead to an interindividual desynchronization of the subjects and to an intra-individual desynchronization of different physiological functions within one subject. Taken together, the observations on the circadian modulation of functions and on the personal tempo as well as the data of temporal production strengthen the concept of an independence of temporal mechanisms in different functional domains (Pöppel & Bao, 2014), and demonstrate also the power of environmental variables as indexed by social factors. These observations may be important for long-term projects like expeditions into space when participants are no longer exposed to the natural geophysical cycle; the light–darkness cycle as the most dominant zeitgeber is no longer available unless simulated. In such a situation, physiological and psychological synchronization on different operating levels is essential for success and it might be jeopardized by psychological outliers no longer sharing the same time window.

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