Temporal integration in auditory sensory memory: neuromagnetic evidence

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Accepted for publication: 4 December 1995

Abstract

The cortical mechanisms of auditory sensory memory were investigated by analysis of neuromagnetic evoked responses. The major deflection of the auditory evoked field (N100m) appears to comprise an early posterior component (N100mP) and a late anterior component (N100mA) which is sensitive to temporal factors. When pairs of identical sounds are presented at intervals less than about 250 msec, the second sound evokes N100mA with enhanced amplitude at a latency of about 150 msec. We suggest that N100mA may index the activity of two distinct processes in auditory sensory memory. Its recovery cycle may reflect the activity of a memory trace which, according to previous studies, can retain processed information about an auditory sequence for about 10 sec. The enhancement effect may reflect the activity of a temporal integration process, whose time constant is such that sensation persists for 200–300 msec after stimulus offset, and so serves as a short memory store. Sound sequences falling within this window of integration seem to be coded holistically as unitary events.

Keywords: Audition; Evoked response; Magnetoencephalography; Sensory memory; Temporal integration

1. Introduction

Evoked responses normally decrease in amplitude if the stimulus is repeated within a short interval. The neural systems generating the response are supposed to suffer a temporary loss of excitability or an increase of inhibition, which recovers over a silent interval. The progressive increase in amplitude of an evoked response as inter-stimulus interval (ISI) increases is therefore referred to as a "temporal recovery function." Hari et al. (1987) determined the temporal recovery function of N100m, the most conspicuous deflection of the auditory evoked magnetic field, whose source appears to lie in supratemporal cortex. The amplitude of N100m increased as the interval between onsets of noise bursts increased from 1 to 9 sec.

We were therefore surprised to observe that when pairs of sounds were presented at intervals of less than 500 msec, the N100m response to the second sound appeared to be enhanced. In our first investigation (Loveless et al., 1989), identical noise bursts of 50 msec duration were delivered in pairs to the left ear at inter-pair intervals (IPIs) of 1.2–1.4 sec. Stimulus onset asynchrony (SOA) within the pair was varied from 70 to 500 msec. At the longest SOAs, the responses to the second stimulus were comparable to those to the first, but were clearly enhanced at SOAs of 150 and 230 msec; at the same time peak latency was prolonged from 100 msec to about 120 msec. Since the duration of the noise burst was constant in this experiment, it was unclear whether the important parameter was time between onsets of the two stimuli or time between offset of the first and onset of the second. Therefore in a second investigation (Loveless and Hari, 1993) we presented pairs of noise bursts at a constant SOA of 420 msec while varying the duration of the first stimulus. For IPIs comparable to those of the previous experiment, amplitude of the second response was appreciably enhanced when duration of the first stimulus was 240 msec rather than 100 or 400 msec – that is, when the silent interval between sounds was 180 msec rather than 320 or 20 msec. Latency of the
second response was 140 msec. The combined results show that the amplitude of this response depends on the duration of the silent interval, being greatest when this is of the order of 100–200 msec.

We have suggested (Loveless et al., 1989; Loveless and Hari, 1993) that evocation of this response enhancement might be related to two psychoacoustic phenomena, perceptual grouping and subjective accentuation, which are also elicited by pairs of sounds separated by a few hundred milliseconds. Studies of perceptual grouping show that when a sequence of sounds is separated by alternately short and long intervals, the sequence is parsed by the longer interval, which is experienced as a featureless gap forming part of the perceptual ground, while the shorter interval is experienced as part of the figure bounded by the sounds. There are qualitative differences in the perception of the figure over different ranges of the shorter interval, suggesting that temporal grouping is a complex process involving a number of different mechanisms. At intervals less than about 500 msec, the sounds are the dominant features of the pattern. While they appear successive and distinct, the discontinuity between them is not perceived as a gap; perception is rather of a double sound, a configuration which has been referred to as an "integrated pair" (Fraisse, 1964). Studies of subjective accentuation show that under certain conditions the loudness of a tone is enhanced if it is preceded by another tone. When the tones are identical, loudness enhancement reaches a peak of 4–5 dB for intervals between 100 and 150 msec and then diminishes, being lost when the interval exceeds 250 msec (Irwin and Zwislocki, 1971; Povel and Okkerman, 1981). Some studies report a threshold shift at similar intervals, but recent research suggests that these are largely procedural artefacts and unrelated to loudness enhancement (Miskiewicz et al., 1994).

These perceptual phenomena are probably due to an integrative process in the sensory system (Cowan, 1984). Studies of temporal integration show that perceived loudness increases with stimulus duration up to about 200–300 msec. Studies of persistence show that sensory activity continues for about the same period after stimulus offset. This may account for perception of an integrated pair, since the persistence of the first sound fills the interval between the sounds. Similarly loudness enhancement can be explained by supposing that the input from the second sound summates with the trace of the first. It therefore seems reasonable to suppose that enhancement of the neuromagnetic response to the second sound of a pair also depends upon some persistent effect of the first.

What remains unclear is the nature of the enhanced response itself. Loveless et al. (1989) did not identify sources of the responses, but observed that the distribution of the second response over 7 channels did not differ from that of the first; the enhancement effect therefore appeared to consist of an increase in source strength without a change in source location and was attributed to increased activation of the neuronal population underlying the N100m deflection. However, Loveless and Hari (1993) constructed field maps for two subjects based on measurements with a 24-channel instrument and found a difference in source location between the first and second responses, although its direction was not consistent between subjects; this suggested that the enhancement effect involved activation of a different neuronal population. The aim of the present experiment is therefore to clarify the situation by replicating the paradigm of Loveless et al. (1989), increasing the number of trials so as to obtain reliable estimates of source location and taking advantage of whole-head recording.

2. Method

The subjects were 6 members of laboratory staff (28–49 years; 4 women and 2 men) without histories of hearing loss or neurological disease. One subject suffered from periodic tinnitus but was not using any medication. Informed consent was obtained from each subject.

1 kHz tones of 50 msec duration with abrupt on- and offset were presented in pairs with SOAs of 70, 150, 230, 300, 370 or 500 msec. These intervals were presented in random order within the same block, with the restriction that no SOA could occur more than twice in succession. The IPI varied randomly from 1.2 to 1.4 sec. There was also a control series in which only the first tone was presented. The sounds were led to the subject's left ear through a plastic tube and earpiece. Sound intensity (about 75 dB SPL) was adjusted to be comfortable for each subject. The subject was instructed to ignore the sounds by concentrating on reading a self-chosen book.

Neuromagnetic signals were recorded with the Neuro-mag-122 system (Ahonen et al., 1993) whose helmet-shaped array of 122 planar first-order SQUID magnetometers covers the whole scalp at 61 sites. Each sensor unit contains a pair of gradiometers that measure the two orthogonal tangential derivatives of the magnetic field component normal to the helmet surface at the sensor location. These gradiometers detect the largest signal just above a local brain source, where the field gradient has its maximum.

The subject was seated in a magnetically shielded room with the head supported against the bottom surface of the dewar. Care was taken to ensure that the head was in the middle of the helmet, and the subject was instructed not to move during the measurements. Location of the head with respect to the sensors was determined by measuring the magnetic fields produced by small currents delivered to 3 coils attached to the scalp. Locations of the coils with respect to the pre-auricular points and the nasion were measured with a 3-D digitizer (Isotrak 3S1002, Polhemus Navigation Sciences, Colchester, VT, USA).

The recording bandpass was 0.03–100 Hz (3 dB points; high-pass roll-off 35 dB/decade. low-pass over 80
prestimulus period which furnished a baseline for the measurement of peak amplitudes. The vertical electro-oculogram was recorded simultaneously and epochs in which its activity exceeded 150 µV were rejected from the on-line average. A minimum of 150 responses was averaged for each SOA and for the control series of single tones.

To identify the neural sources of the evoked responses, equivalent current dipoles (ECDs) best describing the measured field pattern at a given latency were found by a least-squares search. After digital low-pass filtering at 40 Hz, a single ECD was first found at the latency of the N100m peak to the first sound of the pair using a subset of channels over the auditory area of each hemisphere. Dipoles were fitted to the data of each hemisphere separately. The goodness of fit (g; Kaukoranta et al., 1986) of the model was also calculated, and only single ECDs explaining more than 75% of the field variance during the response to the first sound of the pair were accepted for further analysis. When a single dipole model explained only the early part of the measured response to the second sound of the pair, and the field pattern during the later part of the deflection was dipolar, an additional source was identified at the latency of the unexplained portion. The criterion for including two dipoles rather than one was thus based on improved explanation during the later part of the measured response to the second sound of the pair and on the considerably improved g value at that given latency. Finally, a time-varying multidipole model was computed where the locations and orientations of the previously found ECDs were kept fixed while the strengths were allowed to change.

Within each hemisphere the effects of SOA on peak amplitudes and latencies of the responses and on dipole moments and latencies were examined with repeated-measures analyses of variance. Post-hoc comparisons were carried out using Fisher’s Protected Least Significant Differences with a significance level of P < 0.05.

3. Results

Fig. 1 shows responses of one subject at SOA of 230 msec. The first tone evokes a response at a latency of about 100 msec, the second a response with double peaks at latencies of about 100 and 150 msec. The peak amplitudes of these responses are largest over the temporal lobes, reflecting activity of the auditory cortices. At some locations over the left (ipsilateral) hemisphere the amplitude of the response to the second tone is larger than that to the first tone.

Fig. 2 shows individual waveforms for all SOAs and for the single (unpaired) stimulus. The maximum responses over the two hemispheres are shown. For all subjects except subject 5, the responses are stronger over the contralateral hemisphere than over the ipsilateral. While there are some individual variations, the response to the second sound compared with that elicited by the first is typically broad and often double-peaked (for example in subjects 1 and 3) at SOAs of 70–300 msec. We therefore attempted to measure the amplitudes and latencies of both peaks. When the response to the second sound consisted of a single broad deflection, and the single dipole model left the later part of the peak unexplained, amplitudes were measured from both early and late parts of the deflection at the same latencies as the peak dipole moments. At the shortest SOA, the response to the second sound overlaps the response to the first. We therefore subtracted the waveform for the unpaired stimulus from the waveform for this 70 msec SOA, and measured the amplitude and latency of responses to the second stimulus from the difference waveform.

Fig. 3 shows the mean (±S.E.M.) peak amplitudes and latencies for the N100m response to the first stimulus and for the early and late peaks of the response to the second stimulus as functions of SOA. SOA had no significant effect on N100m to the first stimulus or on the early peak of the response to the second stimulus. However, SOA significantly affected the amplitude of the late peak to the second stimulus (contralateral, F5, 21 = 3.22, P < 0.05; ipsilateral, no measurable ipsilateral response for one subject, F5, 20 = 3.02, P < 0.05). Post-hoc comparisons showed that the late peak was significantly (P < 0.05) smaller for SOAs of 370 and 500 msec than for shorter SOAs in both hemispheres. Its latency was also significantly longer (F5, 21 = 2.64; P < 0.05) for the shorter SOAs (mean = 148 msec) than for the longer SOAs (mean = 136 msec) in the contralateral hemisphere; in the ipsilateral hemisphere there was a non-significant trend in the same direction.

Our initial source analysis showed that the N100m response to the first stimulus could be explained by a single dipole. There were no significant effects of SOA on its strength or latency. This dipole also explained very well the early response to the second stimulus (mean g value 87%), and this response also was not significantly affected by SOA. At long SOAs this single dipole model accounted for most, if not all, of the variance of the second response, but as SOA became shorter more variance was left unexplained. Examination of the residual field showed dipolar patterns at this latency. As pointed out by Hari et al. (1988), residual fields showing systematic patterns indicate that the dipole model is insufficient in explaining the measured data. In the contralateral hemisphere the unexplained variance could be reduced by fitting an additional dipole at the latency of the late peak as shown in Fig. 4 for one subject, but in the ipsilateral hemisphere the signal-to-noise ratio was not usually good enough to allow this. Adding the second dipole at the late peak to the second stimulus improved the explanation at that latency in all
subjects; the mean improvement was from 70% to 90%. In
the contralateral hemisphere SOA had a significant effect
on the dipole strength ($F_{5, 22} = 2.45, P < 0.05$). Post-hoc
comparisons showed that the second dipole was signifi-
cantly ($P < 0.05$) weaker for SOAs of 370 and 500 msecs
than for the shorter SOAs, just as for the peak amplitudes,
but there was no significant change in latency. We desig-
nate the early and late components of N100m as N100m$^P$
and N100m$^A$ respectively, since (as we show below) their
source locations differ in the postero-anterior direction.

In addition, Fig. 4 shows that the two-dipole model also
improves the explanation of the late part of the response
to the first stimulus. It thus seems that the N100m response
consists of early and late components, though in some
cases the relative contribution of the second source is so
weak that the response can be adequately explained by
the first. In order to make this latent component manifest, we
re-analysed the data in a different way. We assumed that
changes in SOA elicited changes in source strength but not
in dipole location. The source locations were determined
from the responses obtained at the 150 msec or 230 msec
SOA, and these fixed dipoles (N100m$^P$ identified during
the response to the first sound and N100m$^A$ during the
response to the second sound) were applied to explain all
the data with time-varying strengths. This analysis gave
strengths of the two dipoles as functions of time, as shown
in Fig. 5 for one subject. Here the late response to the
second stimulus has rather a broad peak, and its strength
appears to be a curvilinear function of SOA, but this trend
was not significant over subjects. SOA had no significant
effect on the latency or strength of the second dipole for
the first stimulus.

Fig. 6 shows the mean (+ S.E.M.) locations and orien-
tations of the ECDs for the early and late components. The
source of the second component was significantly anterior
to that of the first (paired $t$ test = 3.6, $P < 0.05$; mean

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Fig. 1. Responses of one subject at SOA of 230 msecs. All 122 signals were recorded simultaneously. The head is viewed from the top and in each response
pair the upper trace illustrates the field derivative along the latitude and the lower trace along the longitude. The inserts show enlarged responses recorded
over the left and right auditory cortices. The two peaks of the N100m response over the right hemisphere are labelled N100m$^P$ and N100m$^A$ because (as
we show below) the source locations of the underlying components differ in the postero-anterior direction.
The latency difference between the N100mP and N100mA responses to the second stimulus is about equal to the stimulus duration, making it feasible that N100mA is an offset response. Offset responses also have a source anterior to onset N100m (Hari et al., 1987). We therefore ran a control series in which the stimuli were identical to those in the main experiment except that we varied the duration of the second stimulus. This duration was either 20 msec, 50 msec (as in the main experiment) or 80 msec.

SOAs were 230 msec or 500 msec. All these conditions were tested separately to avoid mismatch responses. Five subjects were used, three of whom had served in the main

![Fig. 2. Individual waveforms for all SOAs and for the single stimulus, from the channel with the maximum response over each hemisphere. The waveforms are in order of increasing SOA from top downwards, with the single stimulus at the bottom.](image)

![Fig. 3. Mean (± S.E.M.) peak latencies and amplitudes for the N100m response to the first stimulus (filled squares), and for the early peak (open squares) and late peak (circles) of the response to the second stimulus, as functions of SOA.](image)

![Fig. 4. Top: N100mP and N100mA field patterns at their peak latencies displayed over the sensor arrays viewed from the right; SOA was 300 msec. The squares show the locations of the sensor units, and the arrow midpoints indicate the ECD source locations. The isocontours are separated by 50 fT, and the shaded areas indicate magnetic field emerging from the head. The corresponding strengths of the N100mP and N100mA sources as functions of time are shown on the right. Bottom: measured responses (thin dashed lines) of the same subject from one channel and signals predicted by the 1-dipole (thin solid lines) and 2-dipole (thick solid lines) time-varying models.](image)
experiment. The results showed that two sources were needed to explain the second response when the SOA was 230 msec, but not when it was 500 msec. The mean latency of the second component did not change significantly as a function of the duration of the second tone (mean latencies ± S.E.M.: 143.6 ± 8.4; 145.2 ± 12.7; 149.4 ± 13.4 for durations of 20, 50 and 80 msec respectively). This shows that N100m^A is not an offset response but is linked to stimulus onset.

4. Discussion

The object of the experiment was to obtain evidence about the nature of the enhanced N100m response evoked by the second of a pair of sounds in our previous investigations. It transpires that this response is not unitary, but the result of overlap between an early posterior response (N100m^P) and a later anterior response (N100m^A) at latencies of about 90 and 140 msec in the contralateral hemisphere, and 110 and 160 msec in the ipsilateral hemisphere. N100m^P is remarkably invariant in amplitude and latency; the “enhancement effect” is due solely to the increased amplitude of N100m^A at short SOAs. It also appears that the response to the first sound consists of the same posterior and anterior components with peak latencies of about 90 and 110 msec.

These results can be related to recent evidence that N100m can be dissociated into subcomponents with different source areas. Lü et al. (1992a) presented isochronous trains of tones at ISIs of 1.2 or 6 sec. In the short ISI condition, the magnetic response in the contralateral hemisphere could be accounted for by a single dipole identified as N100m; but at the long ISI a second component (L100m) was identified and attributed to a source about 2 cm inferior to that of N100m in the posterior temporal lobe. The recovery cycle of L100m was appreciably longer than that of N100m. Lü et al. (1992b) showed that ISI had a similar effect on the behaviourally measured duration of auditory sensory memory. Sams et al. (1993) presented tones at ISIs from 0.75 to 12 sec and were able to fit two sources to the rising and falling slopes of N100m, but could not identify a source as lateral as L100m. They located both sources in supratemporal cortex, separated by about 1 cm in the antero-posterior direction; this agrees with the source locations of N100m^P and N100m^A in the present study. At short ISIs the major contribution to N100m came from the posterior source, which peaked about 30 msec earlier than the anterior. These subcomponents also showed different recovery times. The posterior subcomponent reached asymptote at about 6 sec, whereas the anterior had a longer time constant, suggesting a trace duration of at least 12 sec. The latter estimate was closer to that obtained from behavioural evidence for the duration of sensory memory. Mäkelä et al. (1993) showed that the amplitude of N100m increases as a function of ISI from 1 to 16 sec, with a time constant similar to that for the supratemporal component of Lü et al. (1992a). While only one dipole was fitted in each hemisphere, the authors noted that at the 1 sec ISI this did not entirely explain the responses of several subjects, which were of long latency and occasionally double-peaked, suggesting that a second source may contribute to N100m at short ISIs.

These reports agree that there are two subcomponents of N100m, though there is disagreement about their source...
locations. Over the main range of ISI the second source may be considered latent, in that the response is adequately explained by a single dipole; but it becomes manifest at more extreme ISIs, due presumably to its different recovery cycle, which seems more closely related to the duration of auditory sensory memory. We propose that N100m₀ and N100mA can be identified with these subcomponents.

We suggest that the behaviour of N100m₀ and N100mA is affected by several separate mechanisms. Firstly, it is affected by the recovery cycles of these subcomponents, which depend upon IPI and SOA, and probably also upon the similarity of the stimuli, though it is not known how this affects the subcomponents. The IPI of the present experiment is close to the interval at which Mäkelä et al. (1993) found that a single source was not always adequate. The first stimulus of our pairs evoked subcomponents whose latency difference was comparable to that found by Sams et al. (1993). The response to the second stimulus also is affected by IPI (Loveless and Hari, 1993). It is possible that the long latency of N100mA at SOAs of 70–230 msec is due to its recovery cycle. However, we are not aware of any evidence that the latencies of the subcomponents are functions of ISI. The latency of undifferentiated N100m is little affected by ISI except for some irregularity at short ISI (Hari et al., 1987; Mäkelä et al., 1993) which can probably be attributed to changes in the relative strengths of N100m₀ and N100mA.

The long latency of N100mA might also be due to masking. The present experiment is formally analogous to the forward masking paradigm. At intervals less than 20 msec, forward masking is thought to be mainly peripheral, but masking can last for up to 200 msec and then seems likely to be a central effect due to persistence of the pattern of excitation set up by the masker. This internal representation is more selective than simultaneous masking, due perhaps to lateral suppression (Moore, 1983; Zwicker and Fastl, 1990). We suppose that in forward masking the response evoked by the second stimulus becomes broader and later, as was shown for simultaneous masking by Hari and Mäkelä (1988). However, these authors noted a dissociation of sensation and evoked response. In particular, simultaneous masking by a continuous tone affected detection of another, but did not alter the amplitude of N100m. In fact, Gerken (1993) reviews evidence suggesting that a continuous tone of moderate intensity may actually enhance the amplitude of some cortical potentials evoked by brief acoustic stimuli. Loveless et al. (1994) observed that transient responses to both onsets and offsets of brief tones were delayed in latency but enhanced in amplitude when a continuous tone of the same frequency was presented to the other ear. They suggested that the prolonged latency was due to forward masking, and the enhanced amplitude to facilitation by some neural process reflected in the sustained field evoked by the continuous tone. We suppose that if simultaneous facilitation is possible, so is forward facilitation, and that the enhanced amplitude of the second response is due to a mechanism different from that responsible for changes in latency.

The enhancement of N100mA may therefore provide an objective measure of the persistence due to temporal integration, just as its recovery cycle – granted that it is the same component as that determined by Sams et al. (1993) – agrees quite well with some estimates of the duration of sensory memory. In fact, estimates of the duration of auditory sensory memory from psychological experiments differ appreciably according to the paradigm employed. Cowan (1984) therefore suggests that there are two distinct types of sensory memory: a “short auditory store” which preserves an unanalysed auditory trace for 200–300 msec, and a “long auditory store” which retains more processed information for 10–20 sec. The “short store” is literal and is experienced as sensation, which persists for 200–300 msec regardless of stimulus duration and is integrated over that period. This store can retain information about a brief rapid sequence of sounds, but only holistically, without identifying each component. The persistence of sensation both feeds the temporal integration process which determines a sound’s perceptual qualities, such as loudness, and prolongs an information extraction process which improves discriminability (Cowan, 1987). In contrast, the “long store” is not literal and is experienced as vivid memory rather than as continued sensation. It is capable of retaining information about a sequence lasting several seconds. If N100mA has the long recovery cycle of the anterior N100 component of Sams et al. (1993) and reflects temporal integration, it is likely to reflect most directly the activation of the long store, within which we can distinguish two phases, the active phase being the period of sensory input and the passive phase that during which the sensory information remains available (Nätänen, 1992).

Retention of information in the long store permits the analysis of contextual cues and comparisons. Neural processes involved in the comparison of successive stimuli are supposed to be reflected physiologically in mismatch responses (MMRs) which are evoked by changes in such features as frequency, intensity or duration (Nätänen, 1992). Tervaniemi et al. (1994) showed that the occasional omission of the second tone of a pair elicited a mismatch response when the interval between the tones was short (40 or 140 msec) but not when it was long (240 or 340 msec). Thus when both stimuli fell within the “temporal window of integration” (Nätänen, 1992) they were coded as a single event. This suggests that an “integrated pair” deserves its name, being coded as a unitary representation in sensory memory.

MMR thus appears to reflect a comparison between such coded units. It is temporally constrained both by the duration of sensory memory and by the duration of temporal integration, and so provides indirect evidence of these durations. The estimate of duration of sensory memory derived from MMR is comparable with the recovery cycle
of N100 and N100m, suggesting that the amplitude of MMR depends on the strength of the trace (Nääätinnen and Picton, 1987). Previous discussions of the relationship between the magnetic MMR (the mismatch field, MMF) and N100 have recognised that the sources of these responses are appreciably different (Sams et al., 1991; Csépe et al., 1992; Hari et al., 1992; Levänen et al., 1993, 1996). However, it now appears that the sources of MMF and N100mA are closely adjacent.

Sensory input into the long store during the active phase appears to include the effects of persistence due to temporal integration. The process of temporal integration itself may well take place at a lower level of the auditory system; Gerken (1993) cites evidence of altered function in the auditory brain-stem. In this case the fact that temporal integration affects N100mA but not N100mP shows that the afferent systems underlying these responses are at least partially separate.

Sensory input is also likely to be influenced by selective attention. Woldorff and Hillyard (1991) found that the amplitude of electric responses N80 and N125 evoked by tones was interactively affected by attention and ISI. The effect of attention on N80 was weaker for ISIs shorter than 220 msec than for longer ISIs, whereas the reverse was true for N125. This pattern of results suggests that N100mA may be identified with N125 and may be modulated by selective attention to a degree dependent on the persistence of previous stimulation. Thus the effect of attention also depends on the strength of the memory trace.

Mäkelä et al. (1993) confirmed that the N100m response is larger and earlier to contralateral sounds than to ipsilateral sounds and showed that this is true for both left and right hemispheres. Similar ISI effects were found in both hemispheres and for both contralateral and ipsilateral stimuli, implying that the duration of sensory memory is similar in both hemispheres. The present results suggest that the duration of temporal integration is also the same in both hemispheres.

Acknowledgements

The authors are grateful to J.-P. Vasama for participating in the experiments, and to J.P. Mäkelä and Linda McEvoy for constructive comments on the manuscript.

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